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The life cycle of *Paracyclops fimbriatus* (Fischer, 1853) (Copepoda, Cyclopoida)

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SYNOPSIS. The complete life cycle of *Paracyclops fimbriatus* (Fischer, 1853) (Copepoda, Cyclopoida) is redescribed based on cultured material. All 6 nauplius and 5 copepodid stages plus the adults are described in detail. Scanning electron microscopy is used to elucidate the fine structure of some appendages, especially the male antennule, and to study body ornamentation patterns. Sexual dimorphism is first apparent at the copepodid IV stage which has a more robust antennule in the male than in the female.

INTRODUCTION

Paracyclops fimbriatus has been reported from a wide range of freshwater habitats and the geographical records summarised by Dussart & Defaye (1985) indicate a cosmopolitan distribution. It has also been regularly recorded from subterranean waters (Itô, 1954; Pesce & Galassi, 1987) and from waters with a salinity of 31‰(Löffler, 1961). Early reports of this species at great depths in Lake Baikal (Mazepova, 1962) refer to the newly recognized *P. baikalensis* Mazepova, 1978 (Mazepova, 1978).

The genus *Paracyclops* comprises 24 species and subspecies (Dussart & Defaye, 1985; Reid, 1987a, 1987b; Strayer, 1988). The type species, *P. fimbriatus*, was originally described by Fischer (1853), using material from St-Petersburg in Russia. This taxon has been partially redescribed on numerous occasions (for example Kiefer, 1929; Gurney, 1933; Lindberg, 1941; Dussart, 1969; Einsle, 1971). Some descriptions of developmental stages have also been published; one of the most accurate being that of Gurney (1933) but even that gives insufficient data to characterise the copepodid stages. Other descriptions have concentrated primarily on the naupliar instars (Gurney, 1933; Dukina, 1956; Ewers, 1930), but these all lack detail by modern standards. Although the general morphology of cyclopoid naupliar stages has been known for a long time it is only recently that detailed naupliar descriptions of freshwater cyclopoid copepods have been published (Dahms & Fernando 1992, 1993, 1994). Systematic studies on naupliar stages can provide important information on the phylogenetic relationships among copepods (Dahms, 1991a,b).

In the present paper *P. fimbriatus* has been redescribed in detail, including all its developmental stages, in order to provide a base for comparison with other *Paracyclops* species.

METHODS

Adult females of *P. fimbriatus* were collected by plankton net from Regent's Park pond (London) on 29.5.1994. Ovigerous females were kept in plastic dishes filled with fresh water filtered through a 35 μm-mesh net. Water was changed at 2 day intervals until the eggs hatched and the nauplius phase was completed. The adult females were removed after hatching of their egg sacs. Copepodid stages were placed in an aquarium tank in a constant temperature room.

The nauplii were examined as whole mounts. Broken glass-fibres were used to prevent the nauplii from being compressed by the coverslip and to facilitate rotation which allowed viewing from all sides.

Copepodids were dissected in lactophenol. All drawings were made with the aid of a camera lucida using Nomarski differential interference contrast. All measurements were made with an ocular micrometer. Body lengths were measured from the anterior to the posterior end of the body in nauplii, and from the base of the rostrum to the posterior edge of the caudal rami

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in copepodids. Body width is given as the widest part of the nauplius body or the copepodid cephalothorax. In the spine and seta formula of the swimming legs Roman numerals and Arabic numerals are used for spines and setae respectively.

When necessary scanning electron microscopy (SEM) was used to study fine details. Material for SEM was prepared by cleaning specimens in an aqueous solution (one drop in 100 ml of distilled water) of the surfactant detergent RBS pF for 30 min and subsequently sonicating in an ultrasonic cell disrupter for 7 s. Cleaned specimens were washed in 3 changes of distilled water for 5 minutes, dehydrated through a graded acetone series, critical point dried, mounted on aluminium stubs, sputter coated with gold and viewed under an Hitachi S-800 scanning elctron microscope.

RESULTS

Description of Naupliar Stages

Nauplius I

Body length : mean ± standard deviation = 118 ± 2.68 µm (range 113 to 122 µm, n=20), mean body width 75 ± 1.5 µm (range 72 to 77 µm, n=20). Body oval (Fig. 1A), with posterior spinular row on ventral surface and on either side of caudal setae. Ventral surface with 2 paired patches of spinules posterior to labrum. Oval area of integument located posteriorly on ventral surface. Caudal rami represented by pair of naked setae.

Antennule 3-segmented (Fig. 2A). First segment with 1 spinulose seta anteriorly and group of spinules along outer margin. Second segment with 2 setae, distal one spinulose and slightly shorter than proximal plumose one; ornamented with 2 spinular rows along ventral side. Third segment with 2 naked setae distally and 2 spinular rows along ventral margin.

Antenna biramous (Fig. 3A), with 2-segmented protopod comprising coxa and basis. Coxal gnathobase represented by large spine armed with spinular row distally. Basis with 3 small setae along inner margin, 2 of them closely set together in proximal third. Exopod 4-segmented; segment 1 large with 1 spinulose seta and spinular row on outer margin; second segment with 1 long naked seta; third segment with 1 long naked seta and few tiny spinules on outer margin; fourth segment with naked seta proximally and 1 long spinulose seta plus 1 naked seta distally; outer margin with spinular row near proximal seta and single isolated setule apically. Endopod unsegmented; armed with 2 short inner setae and 2 long setae terminally.

Mandible (Fig. 4A) biramous, with 2-segmented protopod comprising small coxa and large basis. Coxal gnathobase with 1 naked seta. Inner margin of basis with 1 spinulose and 1 naked seta; outer margin with minute spinule. Exopod 4-segmented; first to third segments each with 1 plumose seta at inner distal angle; segments 3 and 4 with spinular row along outer margin; apex of fourth segment with long plumose, inner seta and short, naked, outer seta, the latter about as long as segment. Endopod 2-segmented; first segment with two spinulose setae and spinular row on inner distal margin; second segment with 4 naked setae.

Nauplius II

Body length : mean ± standard deviation = 135 ± 7.84 µm (range 113 to 144 µm, n=21), mean body width 88 ± 4.5 µm (range 83 to 100 µm, n=21). Body similar to first nauplius but larger and elongated caudally (Fig. 1B); differing as follows: labrum (Fig. 19C) with some spinules along lateral margin. Caudal region lacking spinular row adjacent to caudal setae.

Antennule (Fig. 2B) armed with third seta on inner terminal edge of distal segment. Antenna (Fig. 3B) with additional small seta at base of large sword-shaped coxal gnathobasic seta. Basis with distal spinular row. Exopod 6-segmented, with 1 extra seta located on minute second segment (arrowed in Fig. 16A). Terminal segment of first nauplius subdivided; segment five with 1 naked seta and additional spinular row distally. Endopod of antenna with 2 plumose setae of equal size and 1 shorter plumose seta terminally, plus 2 inner lateral naked setae.

Coxa of mandible (Fig. 4B) with unilaterally spinulose seta. Additional naked seta present on inner margin of basis. First segment of endopod with one naked seta and one longer plumose seta but with no spinular row on inner distal margin. Second segment of endopod with 4 naked setae and 1 plumose seta. Base of first exopodal segment with additional naked seta.

Maxillule appearing as strong plumose seta (arrowed in Fig. 1B).

Nauplius III

Body length : mean ± standard deviation = 158 ± 6.08 µm (range 155 to 168 µm, n=14), mean body width 105 ± 8.7 µm (range 88 to 117 µm, n=14). Body (Fig. 1C) similar to second nauplius but larger, differing as follows: lateral spinular row on labrum consisting of much stronger spinules. Caudal margin with pair of strong plumose setae adjacent to longer naked setae. Posterior end of body trilobate.

Third segment of antennule (Fig. 2C) acquiring extra naked seta on inner margin. Sixth exopodal segment of antenna (Fig. 3C) with 1 naked inner seta, 1 strong spinulose subapical seta and 1 long spinulose apical seta. Mandible with minor changes in relative lengths of endopodal setae (Fig. 4C).

Nauplius IV

Body length : mean ± standard deviation = 181 ± 8.4 µm (range 166 to 192 µm, n=14), mean body width 125 ± 8.7 µm (range 113 to 144 µm, n=14). Body (Fig. 1D) pear-shaped, differing from Nauplius III as follows: caudal margin with pair of minute spines representing Anlagen of caudal setae. Posterior end of body trilobate and becoming elongated.

Antennule (Fig. 2D) with a longer row of dentiform spinules distally on first segment. Third segment with 2 additional naked setae, plus extra row of long spinules midway along lateral margin.

Coxa of antenna (Fig. 3D) with spinular row midway along outer margin. Basis with 4 setae along inner margin; outer margin with 2 spinular rows on anterior surface and 1 spinular row on posterior surface. Apical segment of exopod with spinular row distally.

Basis of mandible with few mid-anterior surface spinules. Fourth segment of exopod with additional small seta distally (Fig. 4D).

Maxillule (Fig. 1D) bilobed with 2 spinulose and 1 naked seta on inner lobe. Outer lobe with 1 spinulose, 1 plumose and 1 long naked seta.

Nauplius V

Body length : mean ± standard deviation = 210 ± 8.49 µm (range 194 to 226 µm, n=14), mean body width 138 ± 12.08 µm (range 122 to 157 µm, n=14). Body (Fig 1E) similar to nauplius IV, differing as follows: third pair of caudal setae larger.

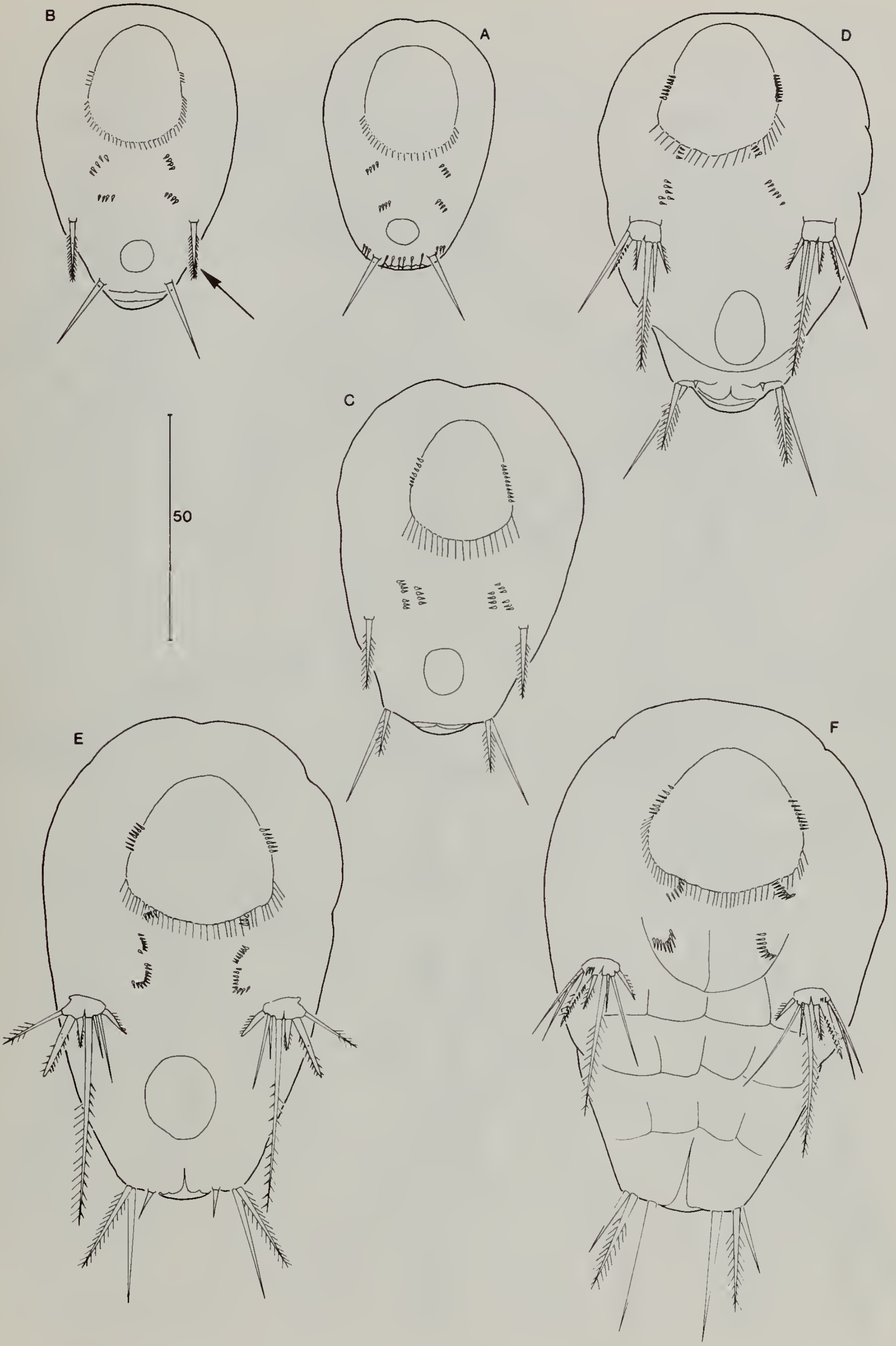

Fig. 1 *P. fimbriatus*. Naupliar stages, ventral view. A, Nauplius I; B, Nauplius II; C, Nauplius III; D, Nauplius IV; E, Nauplius V; F, Nauplius VI. Antennules, antennae and mandibles omitted. Scale bar in μm.

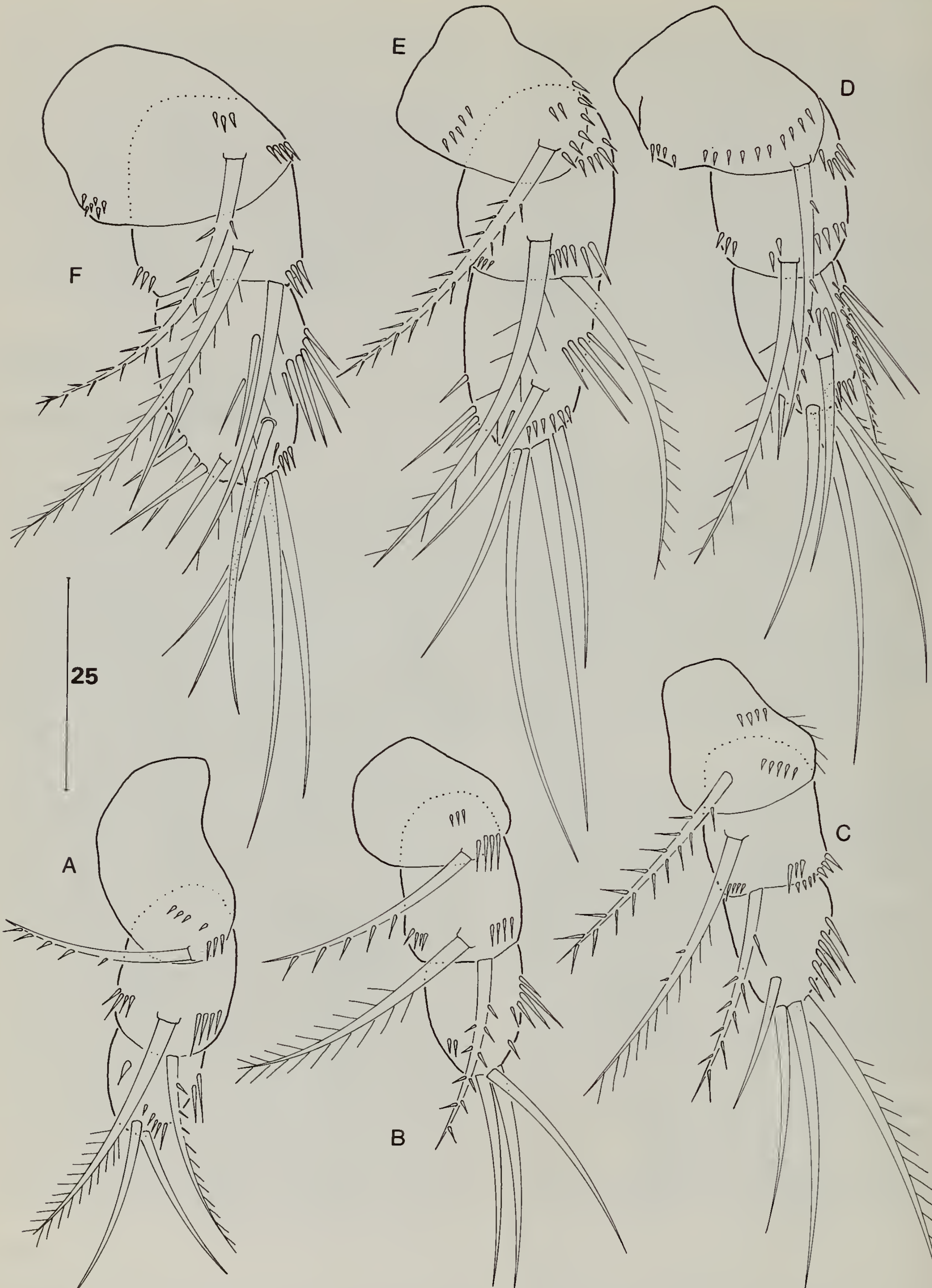

Fig. 2 *P. fimbriatus.* Naupliar antennules, ventral view. A, Nauplius I; B, Nauplius II; C, Nauplius III; D, Nauplius IV; E, Nauplius V; F, Nauplius VI. Scale bar in µm.

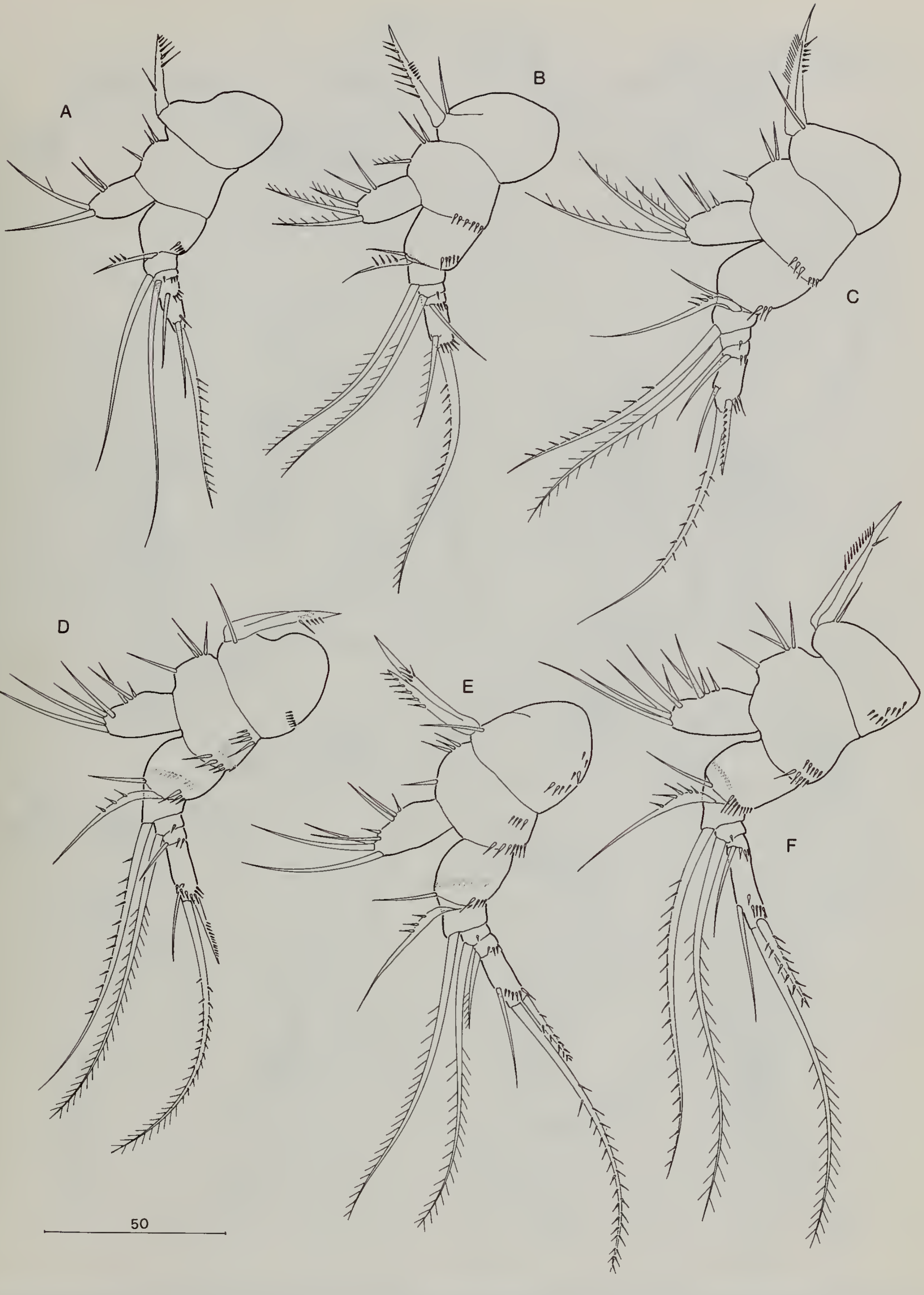

Fig. 3 *P. fimbriatus*. Naupliar antennae, ventral view. A, Nauplius I; B, Nauplius II; C, Nauplius III; D, Nauplius IV; E, Nauplius V; F, Nauplius VI. Scale bar in μm.

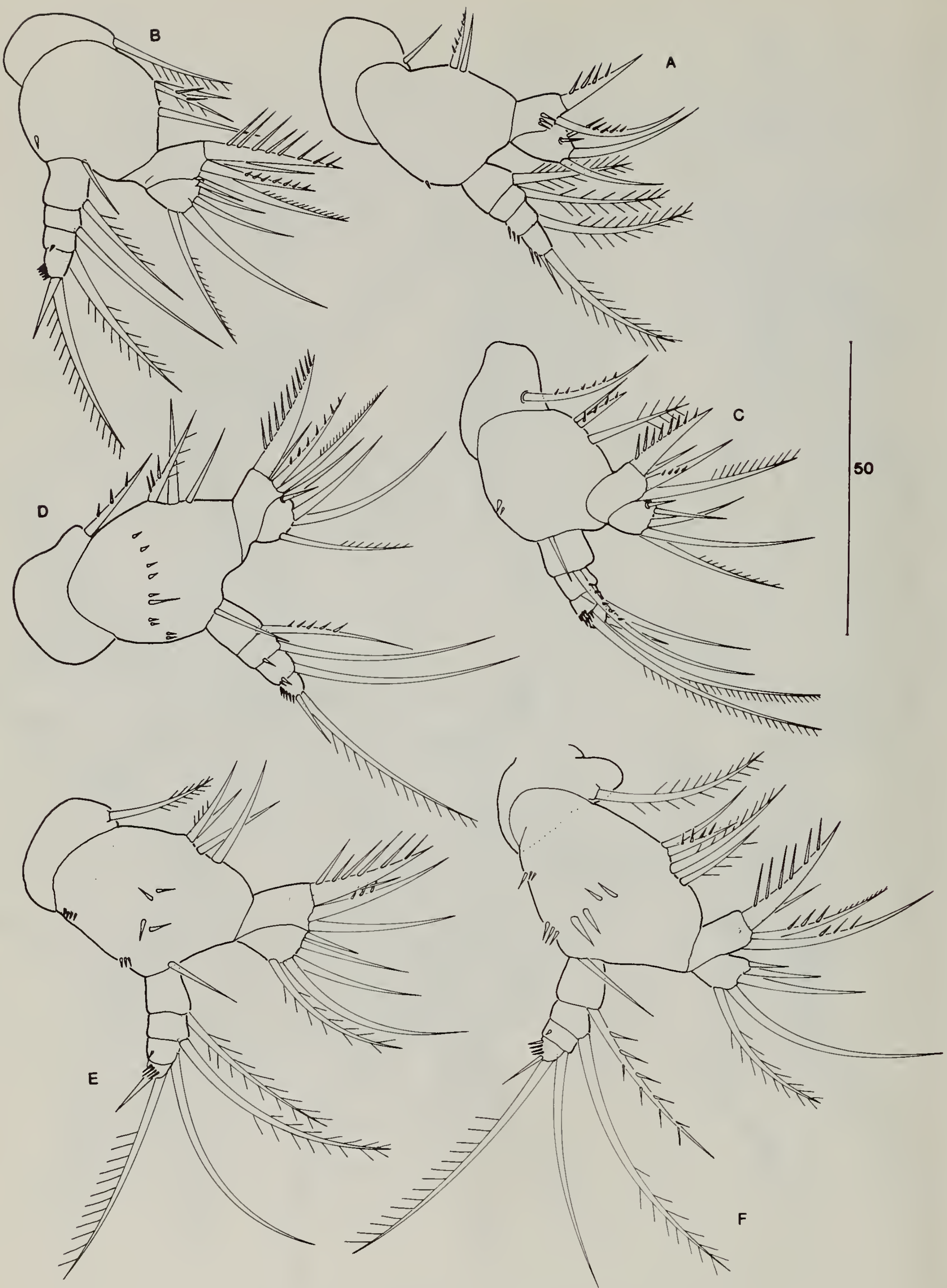

Fig. 4 *P. fimbriatus*. Naupliar mandibles, ventral view. A, Nauplius I; B, Nauplius II; C, Nauplius III; D, Nauplius IV; E, Nauplius V; F, Nauplius VI. Scale bar in µm.

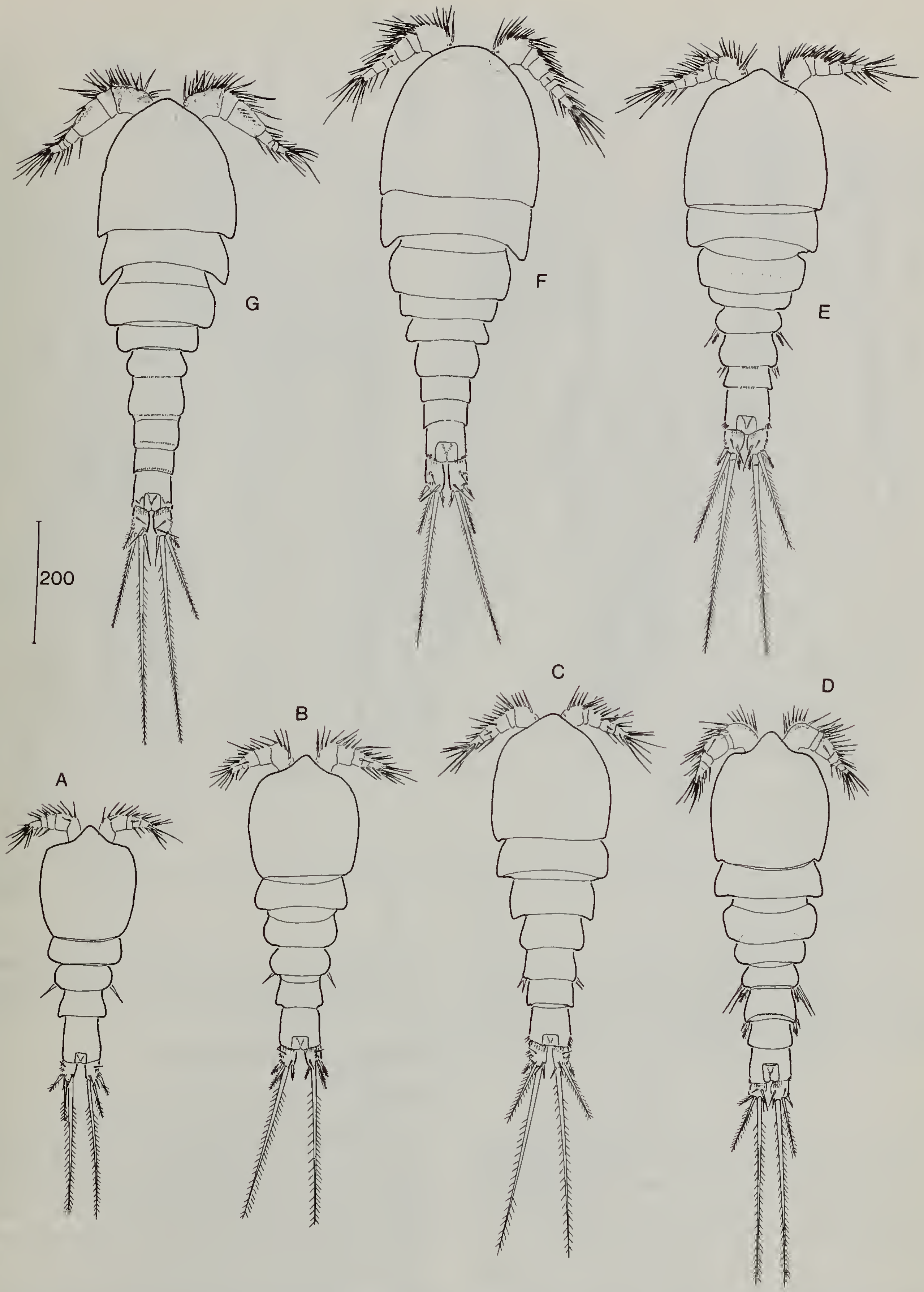

Fig. 5 *P. fimbriatus*. Dorsal view of Copepodid stages I–V. A, Female copepodid I; B, Female copepodid II; C, Female copepodid III; D, Male copepodid IV; E, Female copepodid IV; F, Female copepodid V; G, Male copepodid V. Scale bar in µm.

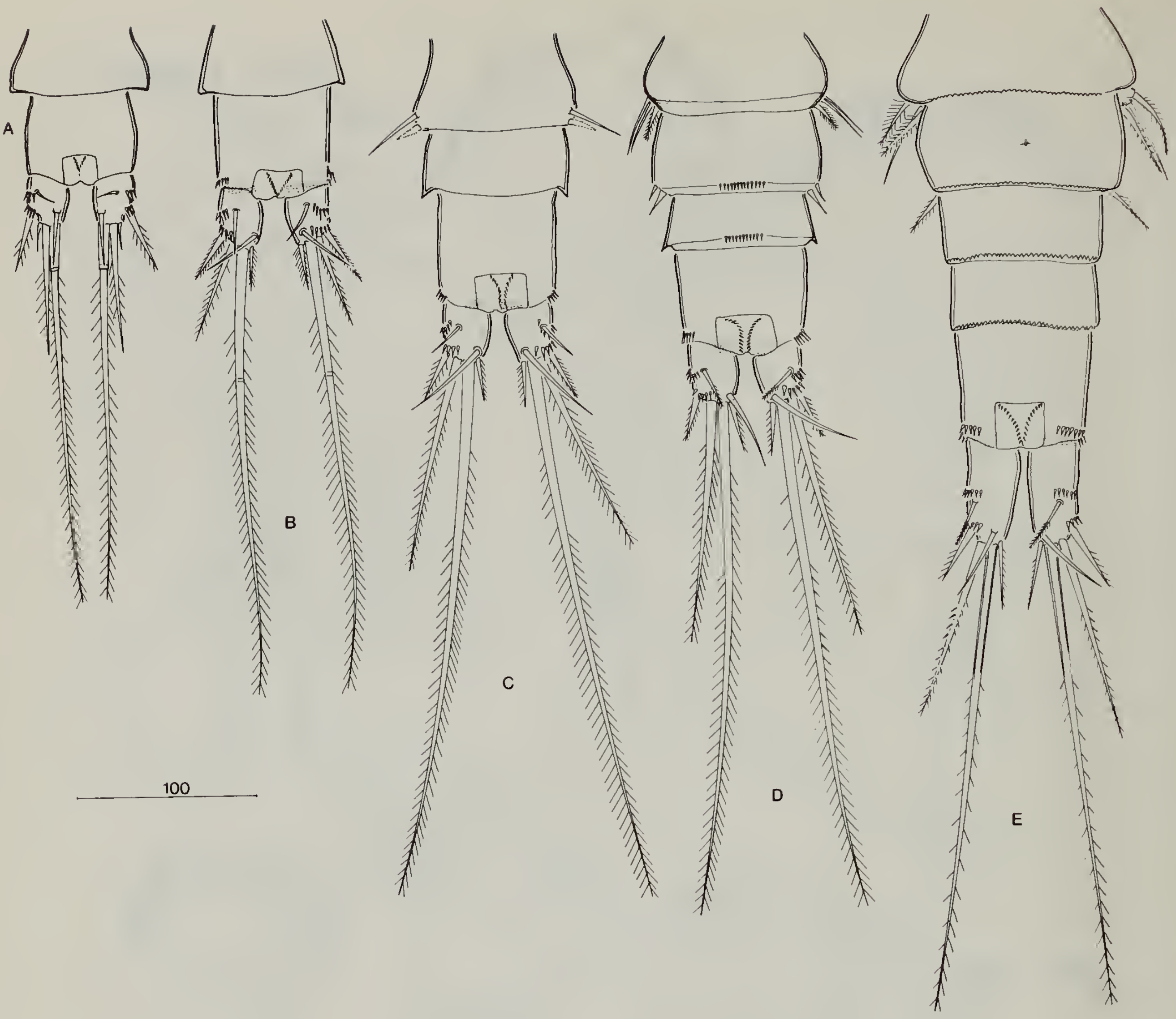

Fig. 6 *P. fimbriatus*. Urosome of female copepodids, dorsal. A, Copepodid I; B, Copepodid II; C, Copepodid III; D, Copepodid IV; E, Copepodid V. Scale bar in µm.

First segment of antennule (Fig. 2E) with spinular row on outer margin. Third segment acquiring 3 small naked setae. Endopod of antenna (Fig. 3E) with additional small naked seta distally. Basis of mandible (Fig. 4E) with 4 setae. Maxillule (Fig. 1E) with 1 new naked seta on inner lobe.

Nauplius VI

Body length : mean ± standard deviation = 241 ± 8.49 µm (range 255 to 224 µm, n=16), mean body width 152 ± 7.28 (range 143 to 162 µm). Body (Fig. 1F) similar to nauplius V, differing as follows: innermost pair of caudal setae longest, middle pair of setae plumose, shortest setae naked and laterally located.

Third segment of antennule (Fig. 2F) with total of 13 setae, including 5 new setae, plus ornamentation of several long spinules. Endopod of antenna with 9 setae (Fig. 3F), with 1 extra seta in proximal group. Mandible (Fig. 4F) with minor changes in ornamentation of basal setae.

Maxillule with 1 new seta on inner lobe, and with 3 spinules on outer margin. Anlagen of post-maxillulary limb pairs apparent on ventral surface of body (Fig. 1F).

Description of Copepodid Stages

Copepodid I

Body length : mean ± standard deviation = 382 ± 11.5 µm (range 373 to 404 µm, n=10), mean body width 146 ± 5.7 µm (range 134 to 152 µm, n=10). Body 5-segmented (Fig. 5A), comprising cephalothorax and 4 postcephalothoracic trunk somites. Second trunk somite with 1 seta at posterolateral angles representing third swimming legs. Antennule, antenna, mandible, maxillule, maxilla, maxilliped and first and second swimming legs present. Caudal rami (Fig. 6A) as broad as long. Each ramus armed with 6 setae, ornamented with spinular row on ventral surface, outermost seta plumose with spinular row at base, 1 naked seta located on dorsal surface posteriorly, 1 short naked seta close to

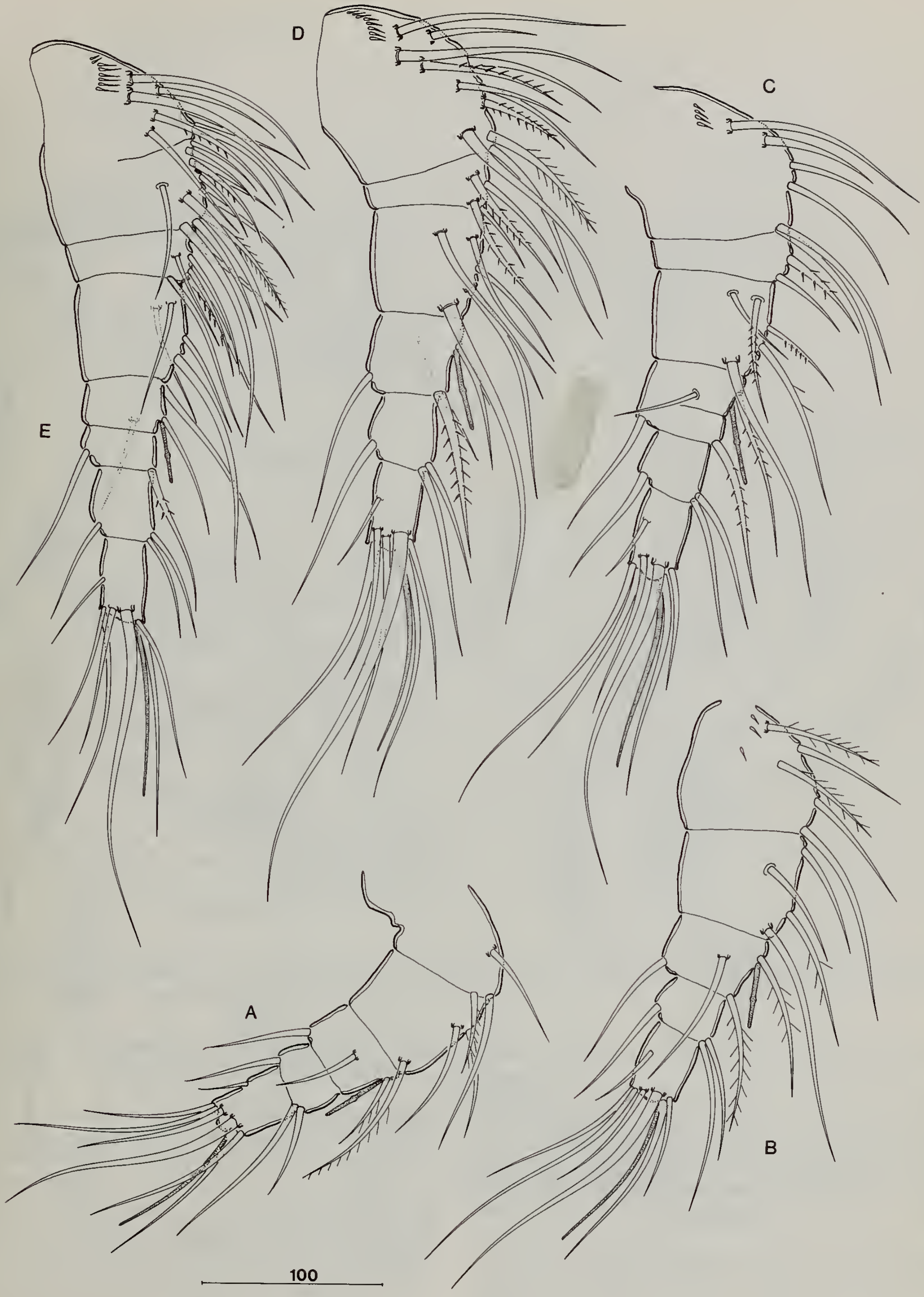

Fig. 7 *P. fimbriatus*. Development of female antennules. A, Copepodid I; B, Copepodid II; C, Copepodid III; D, Copepodid IV; E, Copepodid V. Scale bar in μm.

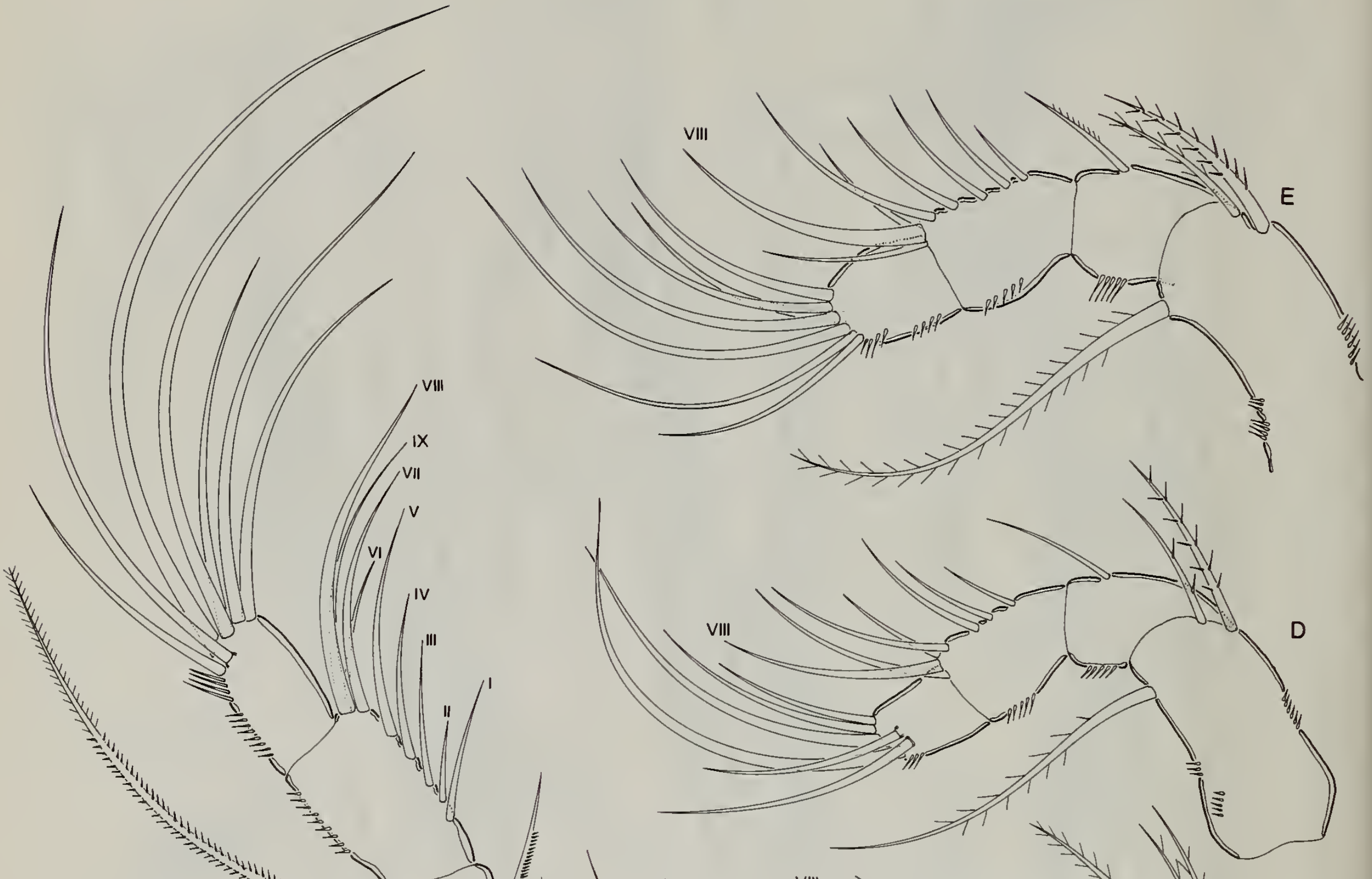

Fig. 8 *P. fimbriatus*. Development of copepodid antennae. A, Copepodid I; B, Copepodid II; C, Copepodid III; D, Copepodid IV; E, Copepodid V; F, Copepodid VI. Scale bar in µm. [Setal numbering scheme of Boxshall & Evstigneeva (1994) is used.]

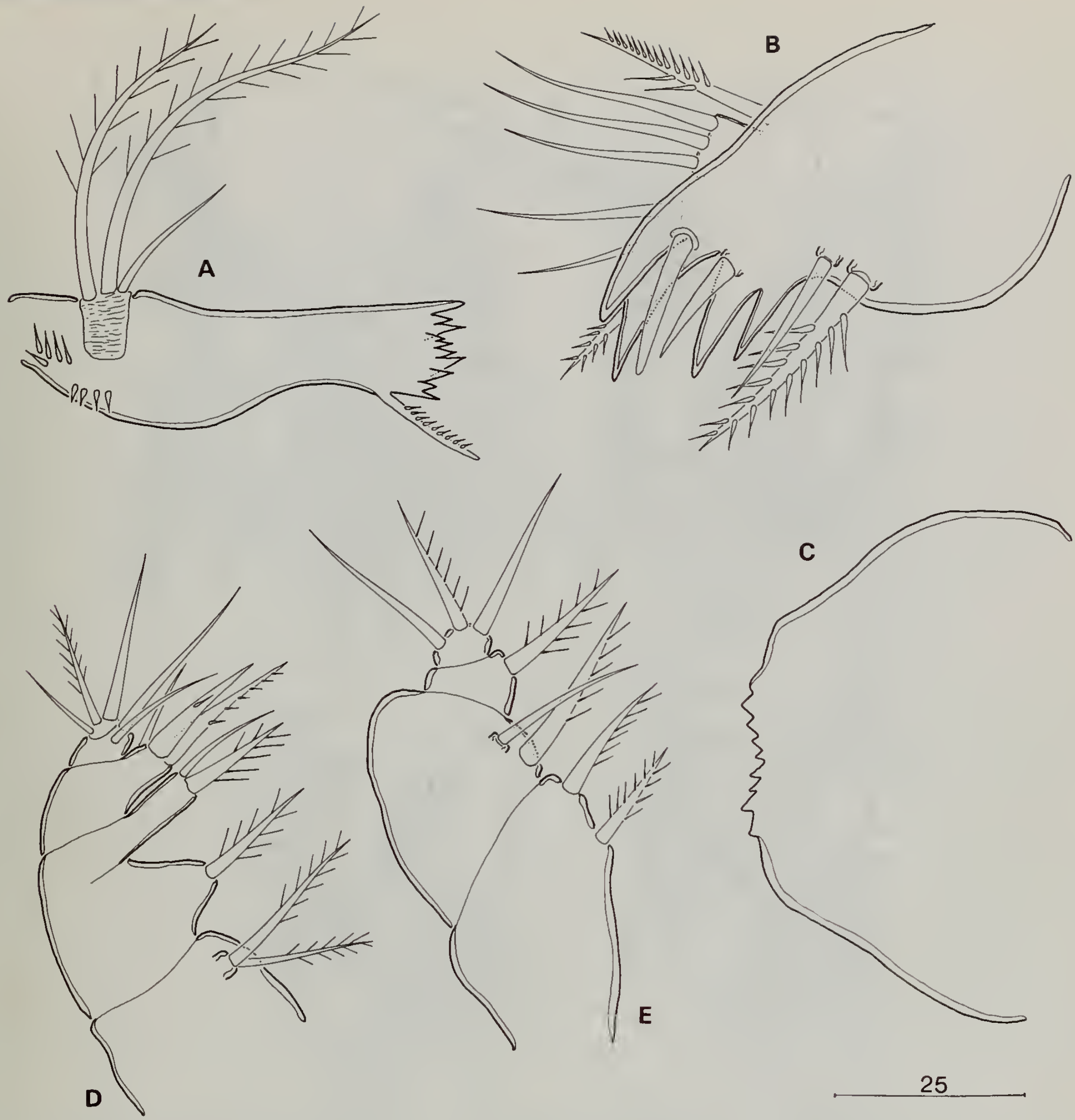

Fig. 9 *P. fimbriatus*. Copepodid I. A, Mandible, posteroventral; B, Maxillule, ventral; C, Labrum, ventral; D, Maxilla, anterior; E, Maxilliped, posterior. Scale bar in µm.

outermost seta, 2 inner plumose setae distally and 1 naked seta on dorsal outer margin. Anal operculum ornamented spinular row.

Antennule 5-segmented (Fig. 7A); aesthetasc at antero-distal angle of apical segment sharing common base with adjacent seta, as in all subsequent stages, including adult. Setal formula 3, 3, 3 + 1 aesthetasc, 3, 7 + 1 aesthetasc.

Antenna 5-segmented (Fig. 8A); coxa unarmed; basis with vestigial exopod bearing 2 naked setae, one apically and one halfway along inner margin. Basis armed with 2 inner angle setae. Endopod 3-segmented; setal formula 1, 4, 6. Labrum (Fig. 9C) with strong denticles along mid posterior margin.

Mandible (Fig. 9A) with well developed gnathobase bearing row of sharp blades medially, and 1 spinulose seta at inner distal angle. Vestigial mandibular palp with 2 long plumose setae and 1 naked seta distally. Inner posterior margin of mandible with two spinular rows.

Maxillule with strong praecoxa and reduced 2-segmented palp (Fig. 9B). Praecoxal endite armed with 4 setae articulating at base and 4 spines fused to segment. Proximal segment of palp derived from coxa and basis, bearing 2 naked and 1 spinulose inner margin setae, plus outer seta representing exopod. Distal segment of palp representing endopod, armed with 3 naked setae.

Maxilla (Fig. 9D) consisting of praecoxa, coxa, basis and 2-segmented endopod. Praecoxa with single indistinct endite armed with 2 plumose setae. Coxa with inner seta at midlength and distal endite bearing strong plumose seta and naked seta apically. Basis with 3 setae distally. Endopod with 2 setae on proximal segment and 3 setae terminally.

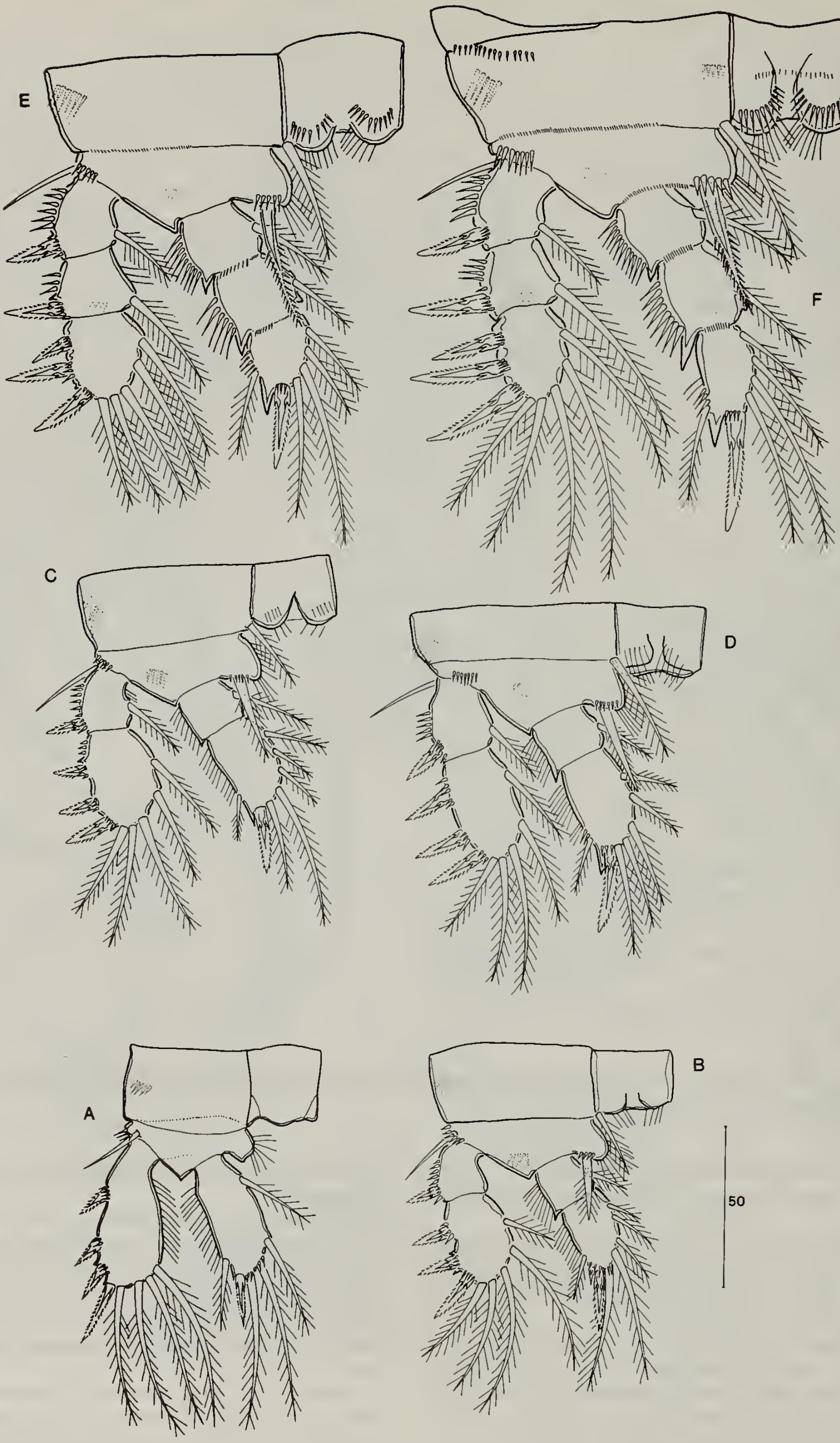

Fig. 10 *P. fimbriatus.* Leg 1, anterior. A, Copepodid I; B, Copepodid II; C, Copepodid III; D, Copepodid IV; E, Copepodid V; F, Copepodid VI (adult). Scale bars in µm.

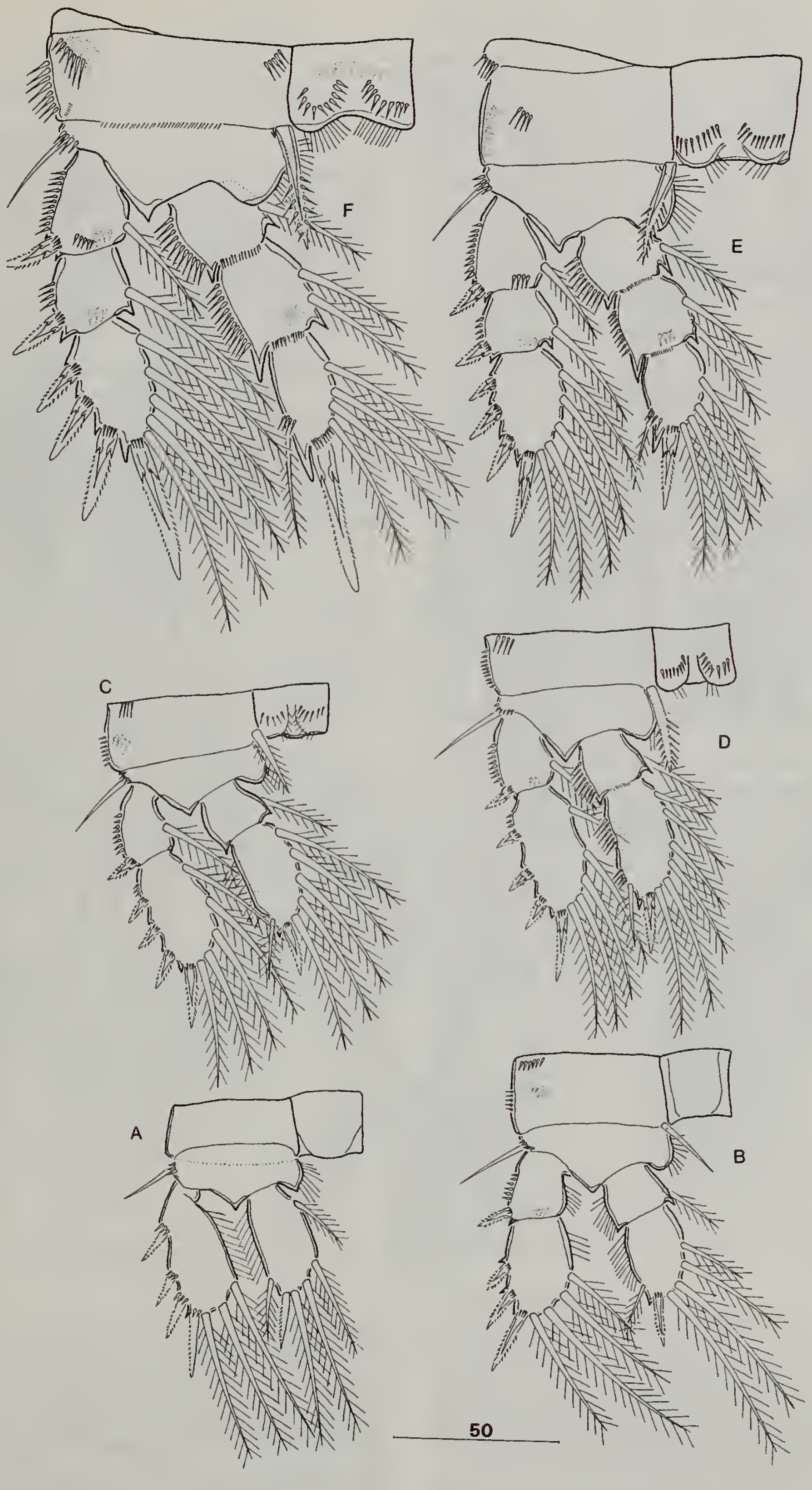

Fig. 11 *P. fimbriatus*. Leg 2, anterior. A, Copepodid I; B, Copepodid II; C, Copepodid III; D, Copepodid IV; E, Copepodid V; F, Copepodid VI (adult). Scale bar in µm.

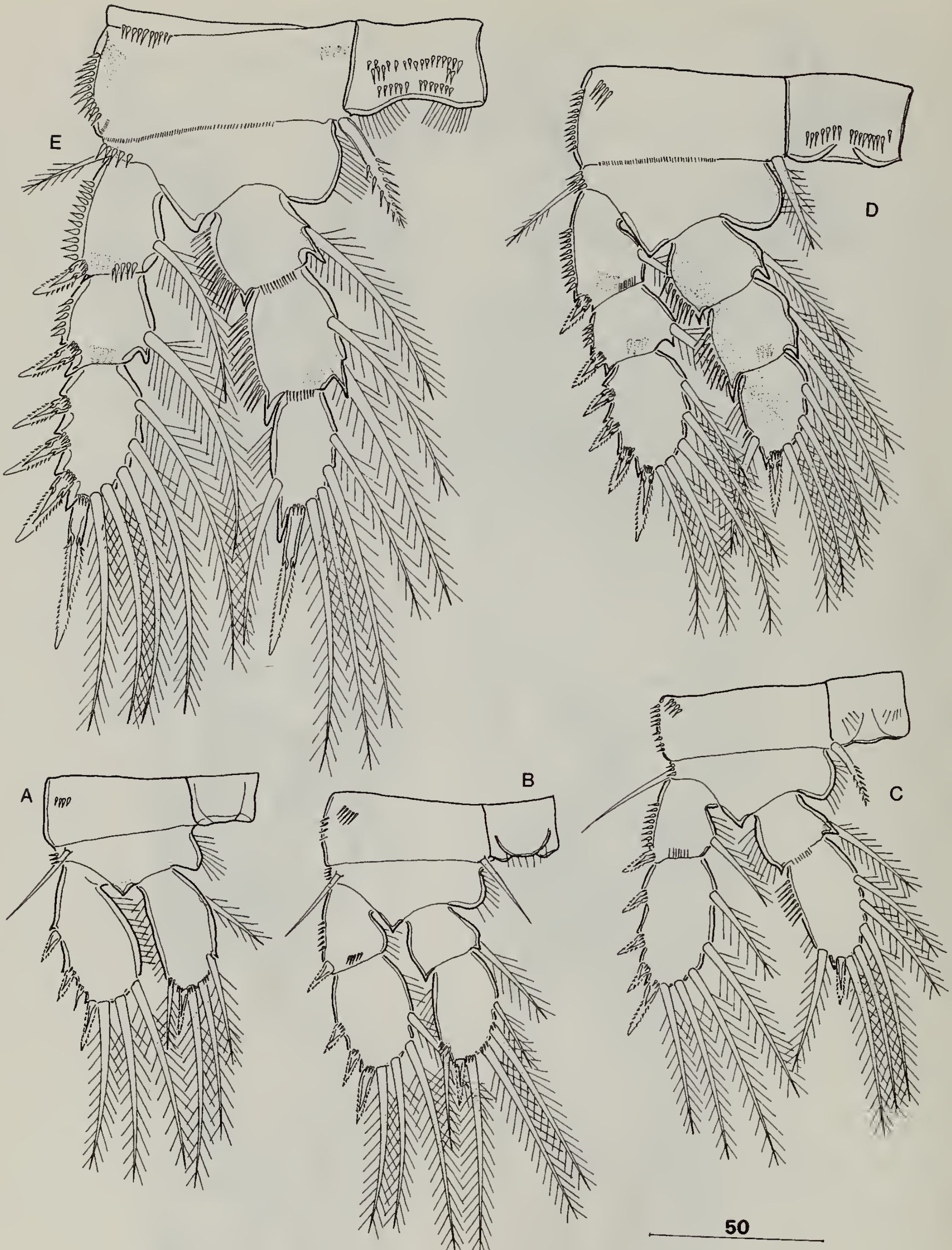

Fig. 12 *P. fimbriatus*. Leg 3, anterior. A, Copepodid II; B, Copepodid III; C, Copepodid IV; D, Copepodid V; E, Copepodid VI (adult). Scale bar in μm.

Maxilliped (Fig. 9E) distinctly 4-segmented, comprising syncoxa, basis and 2-segmented endopod. Syncoxa armed with 2 spinulose setae. Basis with 2 setae. Endopod segment 1 with 1 plumose seta; segment 2 with 3 setae.

Swimming legs 1 (Fig. 10A) and 2 (Fig. 11A) each with 2-segmented protopod. Intercoxal sclerites unornamented. Coxa of leg 1 with spinular row posteriorly. Basis of both legs with outer angle seta ornamented by spinular row at base, inner basal margin with fine spinules. Both legs with 1-segmented rami. Inner margin of exopod and outer margin of endopod of both legs with row of pinnules. Spine and seta formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0–0	1–0	IV,4	1,1+1,3
Leg 2	0–0	1–0	IV,3	1,I+1,3

Copepodid II

Body length : mean ± standard deviation = 455 ± 17.2 µm (range 439 to 488 µm, n=10), mean body width 168 ± 9.1 µm (range 152 to 178 µm, n=10). Differing from Copepodid I as follows: body (Fig. 5B) 6-segmented, comprising cephalothorax and 5 postcephalothoracic trunk somites. Third trunk somite with 1 seta on outer margin representing fourth swimming legs. Last somite with posterior margin spinular rows ventrally and laterally (Fig. 6B).

Antennule with 3 spinules on first segment. Setal formula; 5, 4, 4 + 1 aesthetasc, 3, 7 + 1 aesthetasc (Fig. 7B).

Antenna 4-segmented (Fig. 8B); basis with spinular row near inner margin. Inner setae set close together at distal angle. Vestigial exopod represented by spinulose seta. First endopodal segment with 1 seta, second with 5 setae along distal margin and bearing small spinular row on outer margin. Third endopodal segment with 6 setae distally, ornamented with spinular row on outer distal margin.

Coxa of leg 1 with spinulose seta at inner distal angle (Fig. 10B). Basis with spinulose seta on inner distal margin ornamented with spinular rows at base of inner seta and posteriorly, between exopod and endopod. Intercoxal sclerite ornamented with setules distally. First segment of exopod with spinular row along outer margin. First and second segments of endopod with pinnules along lateral margins.

Coxa of leg 2 (Fig. 11B) with naked seta on inner distal margin; ornamented with spinular rows proximally on outer margin of both anterior and posterior surfaces and along outer margin. First segment of exopod with spinular rows laterally and proximally on posterior surface. Exopodal and endopodal segments with pinnules along inner and outer margins respectively.

Third leg (Fig. 12A) with 2-segmented protopod; coxa with spinular row proximally near outer margin. Basis with naked outer seta; ornamented with tiny spinules at base and hairs along inner margin. Intercoxal sclerite unornamented. Exopod and endopod 1-segmented, bearing pinnules along inner and outer margins respectively. Spine and seta formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0–1	1–1	I–0; III1,5	0–1; 1,I+1,4
Leg 2	0–1	1–0	I–0; III,4	0–1; 1,I+1,3
Leg 3	0–0	1–0	IV,3	1,I+1,3

Copepodid III

Body length : mean ± standard deviation = 511 ± 22.8 µm (range 478 to 534 µm, n=10), mean body width 179 ± 5.3 µm (range 173 to 186 µm, n=10). Differing from copepodid II as follows: body (Fig. 5C) 7-segmented, comprising 4-segmented prosome bearing swimming legs 1 to 4, and 3-segmented urosome (Fig. 6C).

Antennule 6-segmented (Fig. 7C): fourth segment partly divided. Setal formula: 6, 2, 5, 4 + 1 aesthetasc, 3, 7 + 1 aesthetasc. Antenna (Fig. 8C) with spinular row on inner margin of second segment proximally. Second endopodal segment with 6 setae. Labrum with long spinular rows along lateral margins distally.

Exopod of legs 1 (Fig. 10C) and 2 (Fig. 11C) with new seta on inner margin of first segment. Intercoxal sclerite of leg 2 ornamented with rows of setules on anterior surface. Second endopodal and exopodal segments each with new seta. Coxa of third leg (Fig. 12B) with new seta at inner angle and bearing spinular row on outer margin. Intercoxal sclerite ornamented. Exopod and endopod 2-segmented. Leg 4 (Fig. 13A) with 2-segmented protopod; coxa with spinular row on outer margin. Basis with outer angle seta and bearing spinular row on laterally. Exopod and endopod 1-segmented. Intercoxal sclerite unornamented. Leg 5 (Fig. 6C) represented by 2 setae. Spine and seta formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0–1	1–1	I–1;III,5	0–1;1,I+1,4
Leg 2	0–1	1–0	I–1;IV,5	0–1;1,I+1,4
Leg 3	0–1	1–0	I–0;III,4	0–1,1,I+1,3
Leg 4	0–0	1–0	IV,3	1,I+1,3

Female copepodid IV

Body length : mean ± standard deviation = 573 ± 19.5 µm (range 547 to 608 µm, n=10), mean body width 200 ± 14 µm (range 178 to 221 µm, n=10). Differing from copepodid III as follows: body (Fig. 5E) 8-segmented with 4-segmented urosome (Fig. 6D); spinular rows present mid-dorsally along posterior margins of urosomites 2 and 3.

Antennule 6-segmented (Fig. 7D) with entire fourth segment. Setal formula; 11, 4, 5, 4 + 1 aesthetasc, 3, 7 + 1 aesthetasc. Antenna with 2 short spinular rows dorsally on inner side of first segment. Second endopodal segment with 7 setae (Fig. 8D). Mandible with spinular row on ventral margin of coxa. Maxilliped with spinular rows midway along outer margin and on anterior surface near inner setae.

Legs 1–4 with 2-segmented rami (Figs 10D, 11D, 12C, 13B). Coxa of leg 4 with naked seta at inner angle proximally and spinular row on outer margin. Spine and seta formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0–1	1–1	I–1;III,5	0–1;1,I+1,4
Leg 2	0–1	1–0	I–1;IV,5	0–1;1,I+1,5
Leg 3	0–1	1–0	I–1;IV,5	0–1;1,I+1,4
Leg 4	0–1	1–0	I–0;IV,5	0–1;1,II,3

Leg 5 with 3 setae; leg 6 represented by 2 simple setae at posterolateral angle of second urosomite (Fig. 6D)

Male copepodid IV

Body length, (range 565 to 643 µm, n=2), body width, (range 195 to 204 µm, n=2). Differing from female Copepodid IV as follows: anterior part of body (Fig. 5D) not much broader than posterior compared with female; constriction between somites bearing 4th and 5th legs (Fig. 14A) not as distinct.

Appendages as in female fourth copepodid except as follows: antennule 6-segmented (Fig. 15A) but segment 3 broader. Segments 3 and 4 with distinctive short spiniform setation

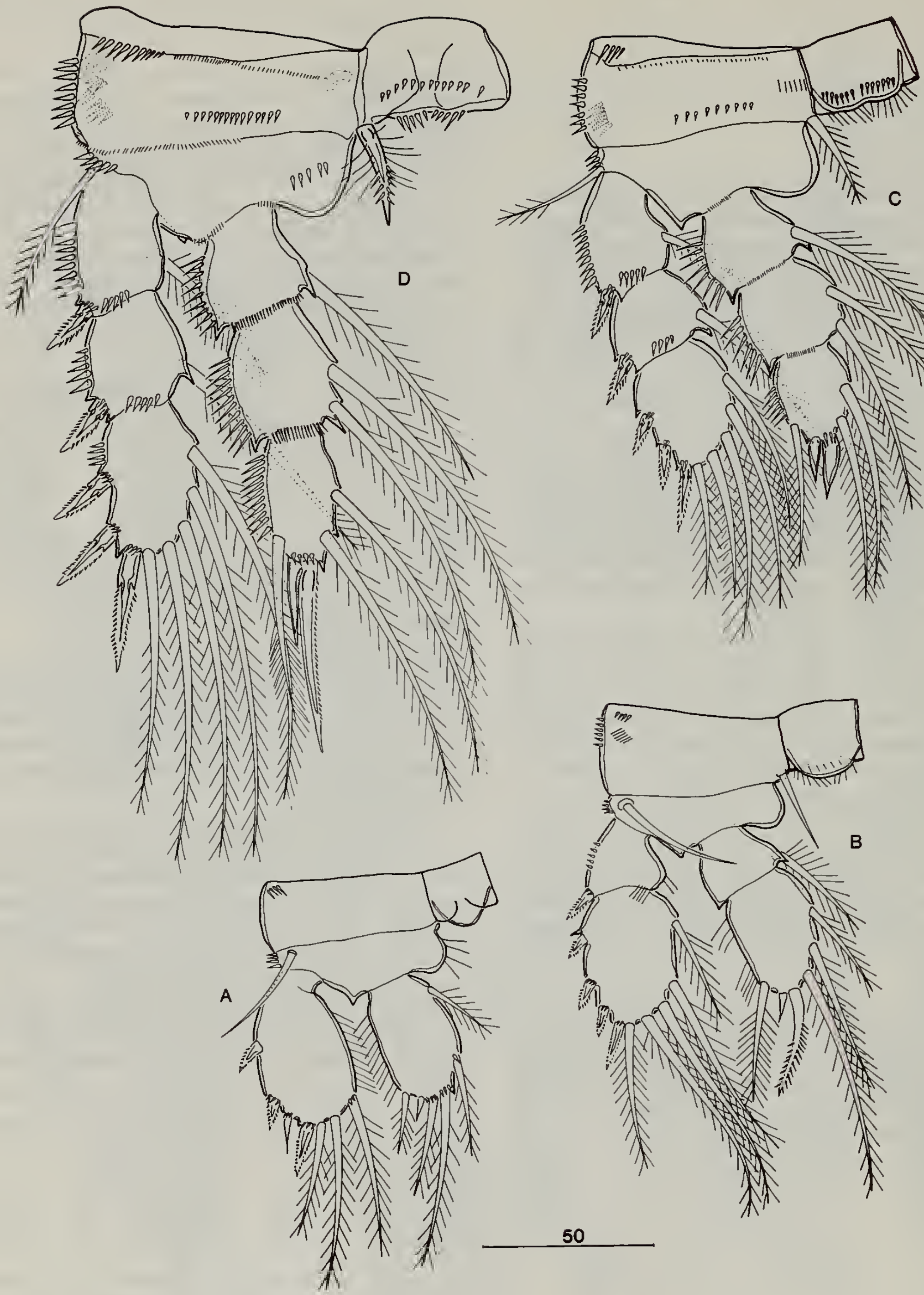

Fig. 13 *P. fimbriatus*. Leg 4, anterior. A, Copepodid III; B, Copepodid IV; C, Copepodid V; D, Copepodid VI (adult). Scale bar in µm.

elements (arrowed in Fig. 16D). Setal formula: 11, 4, 5 + spine, 4 + spine + 1 aesthetasc, 3, 7 + 1 aesthetasc.

Female copepodid V

Body length : mean ± standard deviation = 726 ± 38.47 µm (range 647 to 769 µm, n=10), mean body width 246 ± 12.4 µm (range 217 to 260 µm, n=10). Differing from female Copepodid IV as follows: body 9-segmented (Fig. 5F) with 5-segmented urosome (Fig. 6E); anal somite with dense spinular row along posterior margin extending from ventral surface to dorsal margin, either side of anal slit. Caudal rami about 3 times as long as broad.

Antennule 7-segmented (Fig. 7E) : setal formula; 18, 6, 5, 2 + 1

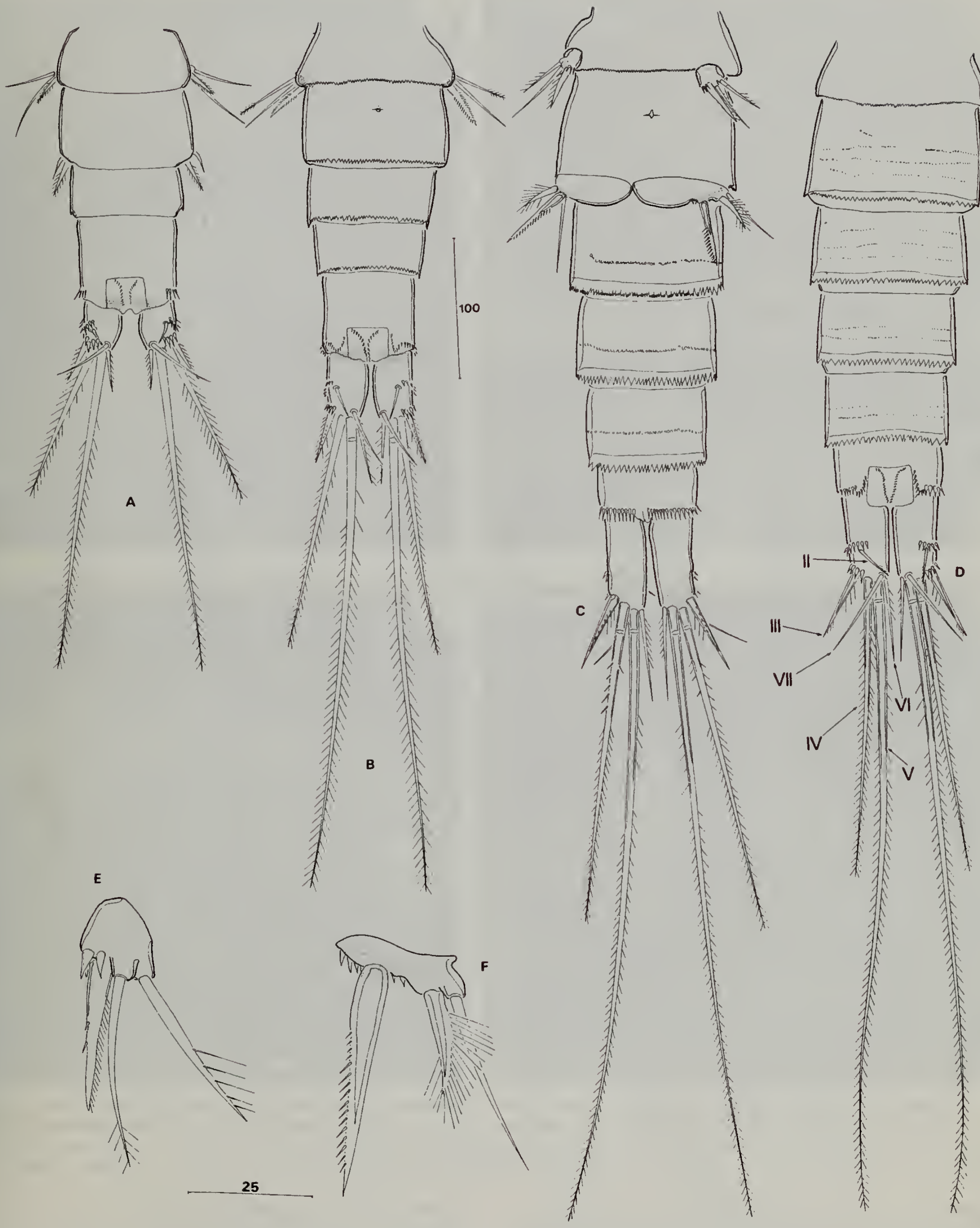

Fig. 14 *P. fimbriatus*. Male. A, Copepodid IV urosome, dorsal; B, Copepodid V, dorsal; C, adult urosome, ventral; D, adult urosome, dorsal; E, Adult leg 5, ventral; F, Adult leg 6, ventral. Scale bars in μm.

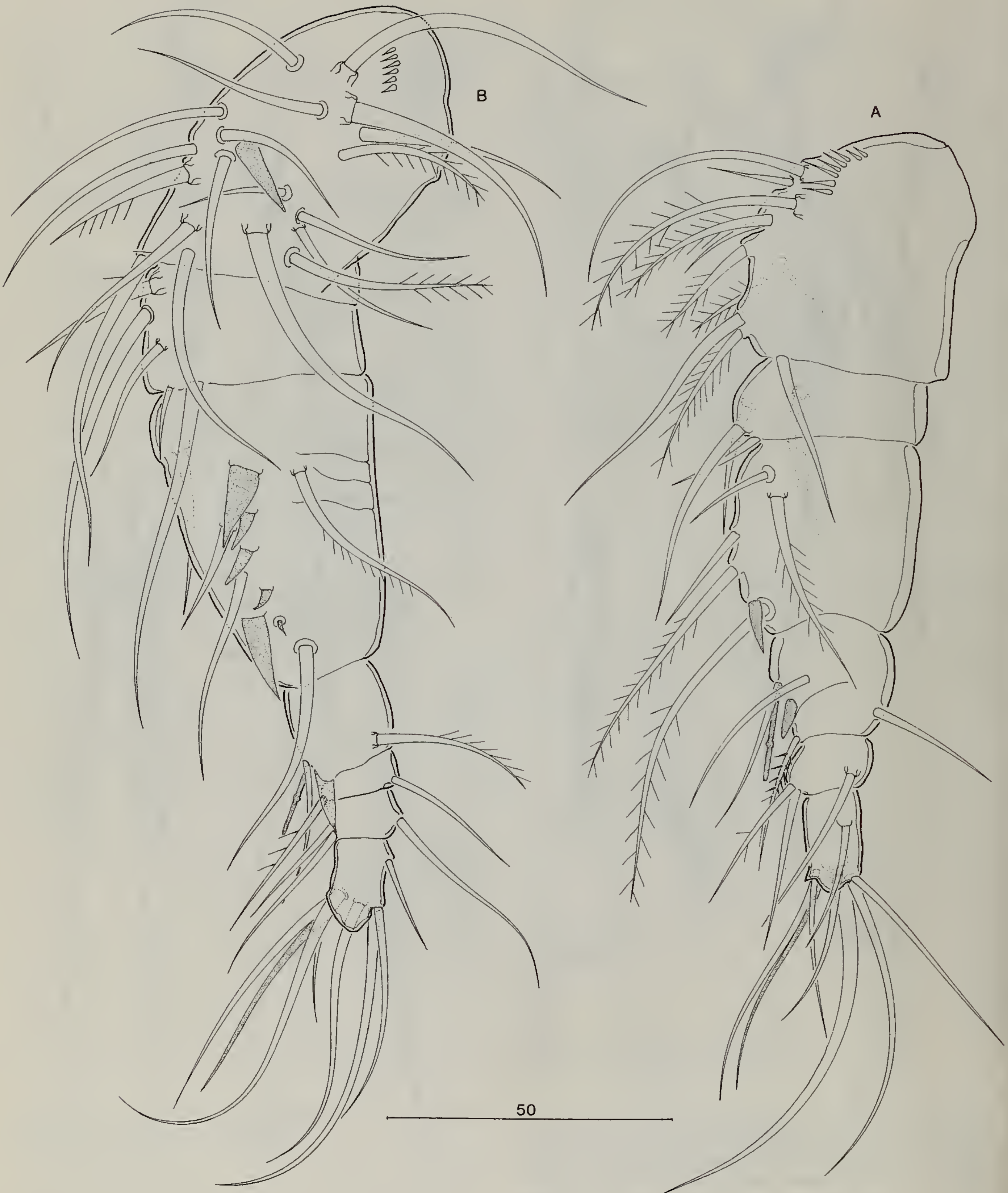

Fig. 15 *P. fimbriatus.* Male antennules, lateral. A, Copepodid IV; B, Copepodid V. Scale bar in μm.

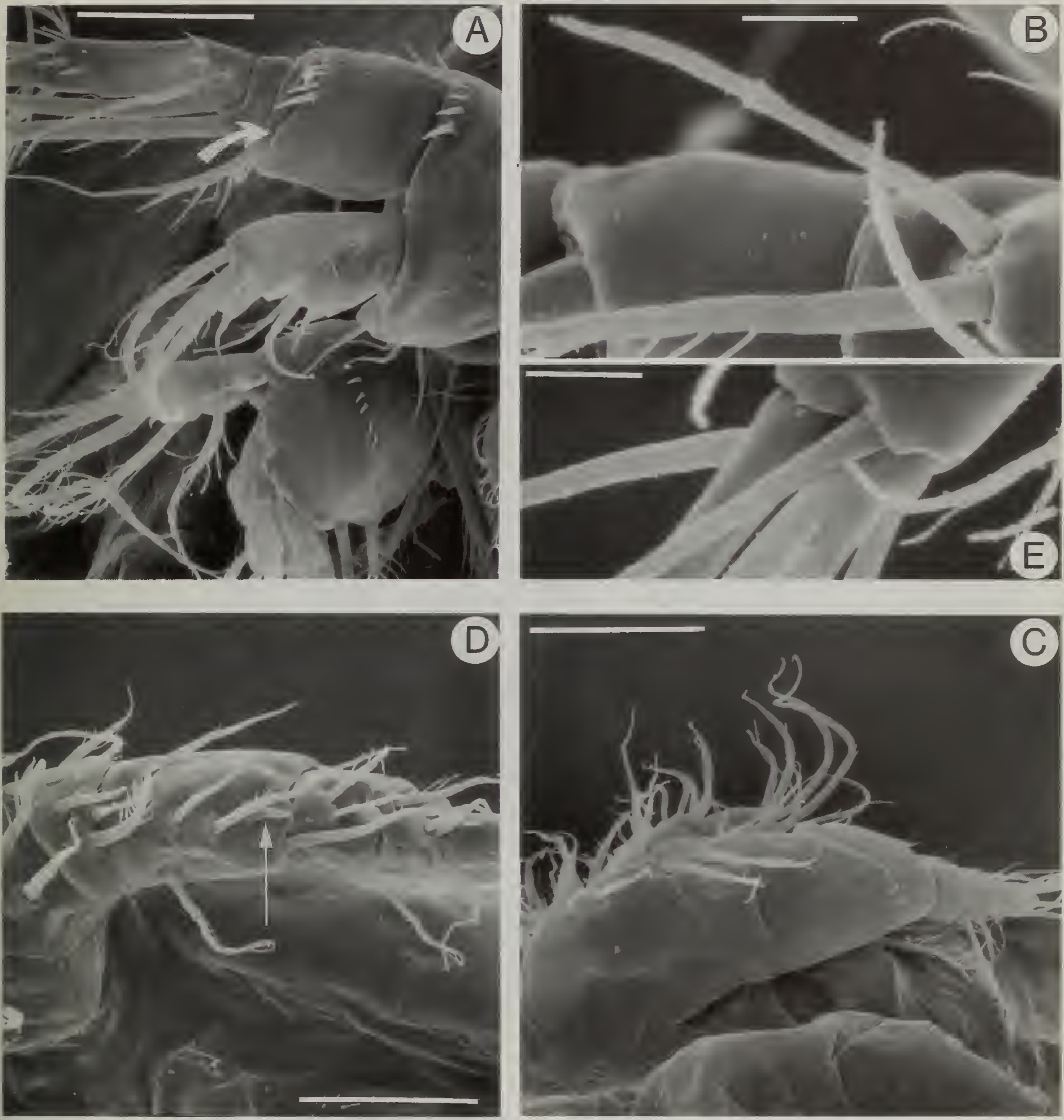

Fig. 16 Scanning electron micrographs of *P. fimbriatus.* A, Nauplius VI antenna, ventral; arrow indicates minute second exopodal segment; B, Adult female antennule, aesthetasc on segment 5; C, Male copepodid V antennule, dorsal; D, Male copepodid IV antennule, ventral; arrow indicates the spine on segment 4; E, Adult female antennule, double fusion on terminal segment, lateral. Scale bars A = 20 µm, B = 5µm, C = 40 µm, D = 25 µm, E = 5 µm.

aesthetasc, 2, 3, 7 + 1 aesthetasc. Second endopodal segment of antenna (Fig. 8E) with 8 setae; distal seta VIII stronger than others. Praecoxal arthrite of maxillule with 5 setae. Proximal spinulose seta ornamented with long spinules. Praecoxa of maxilla with short spinular row on outer margin. Basis of maxilliped with 2 spinular rows laterally.

Leg 1 (Fig. 10E) with 3-segmented exopod and endopod, bearing spinular row posteriorly on second segment of exopod. Intercoxal sclerite with anterior spinular rows distally. Leg 2 (Fig. 11E) with praecoxa bearing spinular row on outer margin. Exopod and endopod 3-segmented: first segment of exopod with proximal spinular row anteriorly, second exopodal and

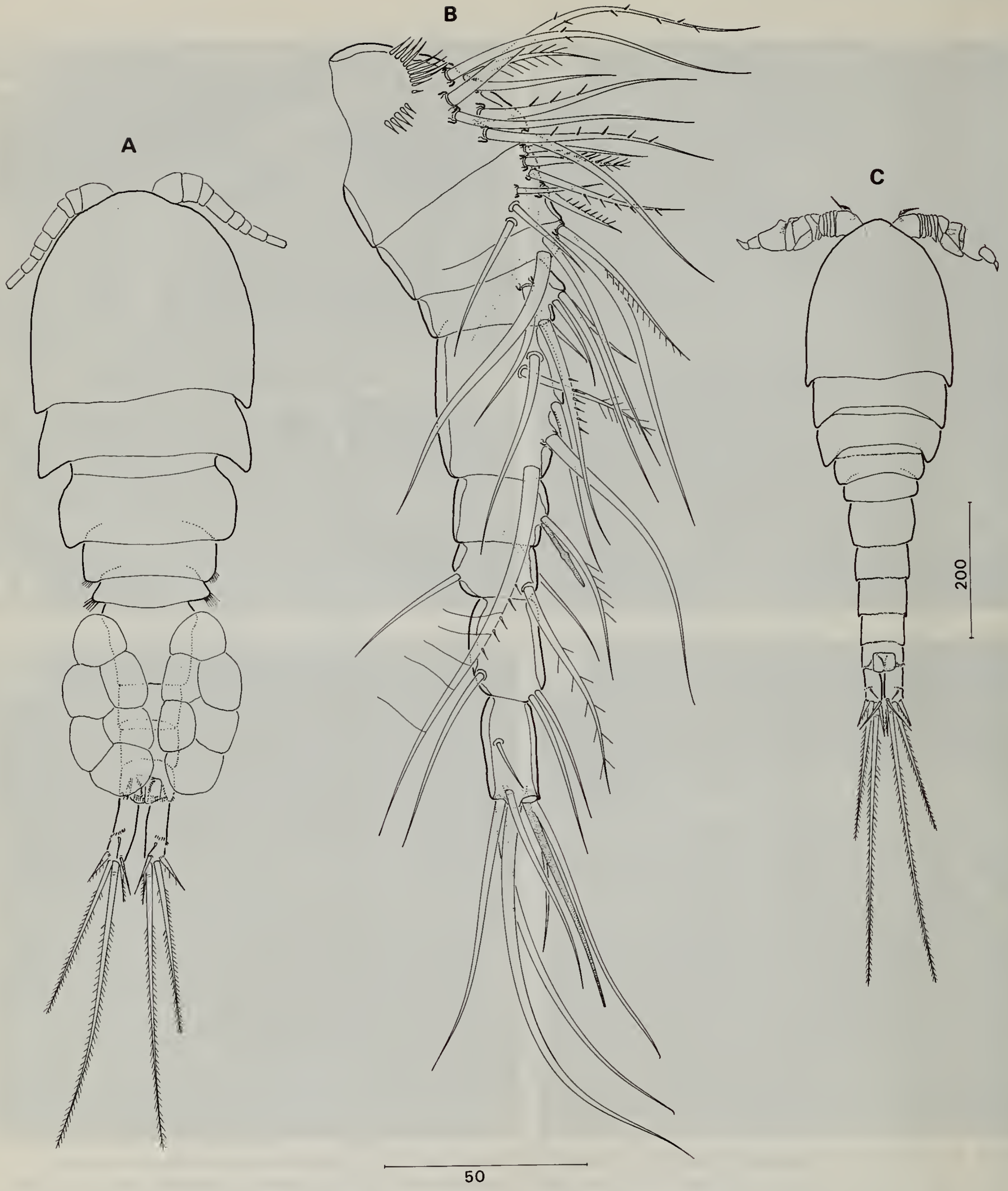

Fig. 17 *P. fimbriatus.* A, Adult female, dorsal; B, Adult female antennule, dorsal; C, Adult male, dorsal. Scale bars in µm.

endopodal segments with spinular rows posteriorly. Leg 3 (Fig. 12D) with 3-segmented exopod and endopod bearing posterior spinular rows on first and second segments of exopod and second segment of endopod. Intercoxal sclerite with transverse spinular row on anterior surface. Leg 4 (Fig. 13C) with praecoxa bearing spinular row on outer margin. Coxa with posterior spinular row near outer proximal angle, spinular row on midanterior surface and very fine spinules along posterior margin. Exopod and endopod 3-segmented: first and second segments of exopod with anterior spinular rows distally. Intercoxal sclerite with transverse spinular row on anterior surface. Spine and seta formula as follows:

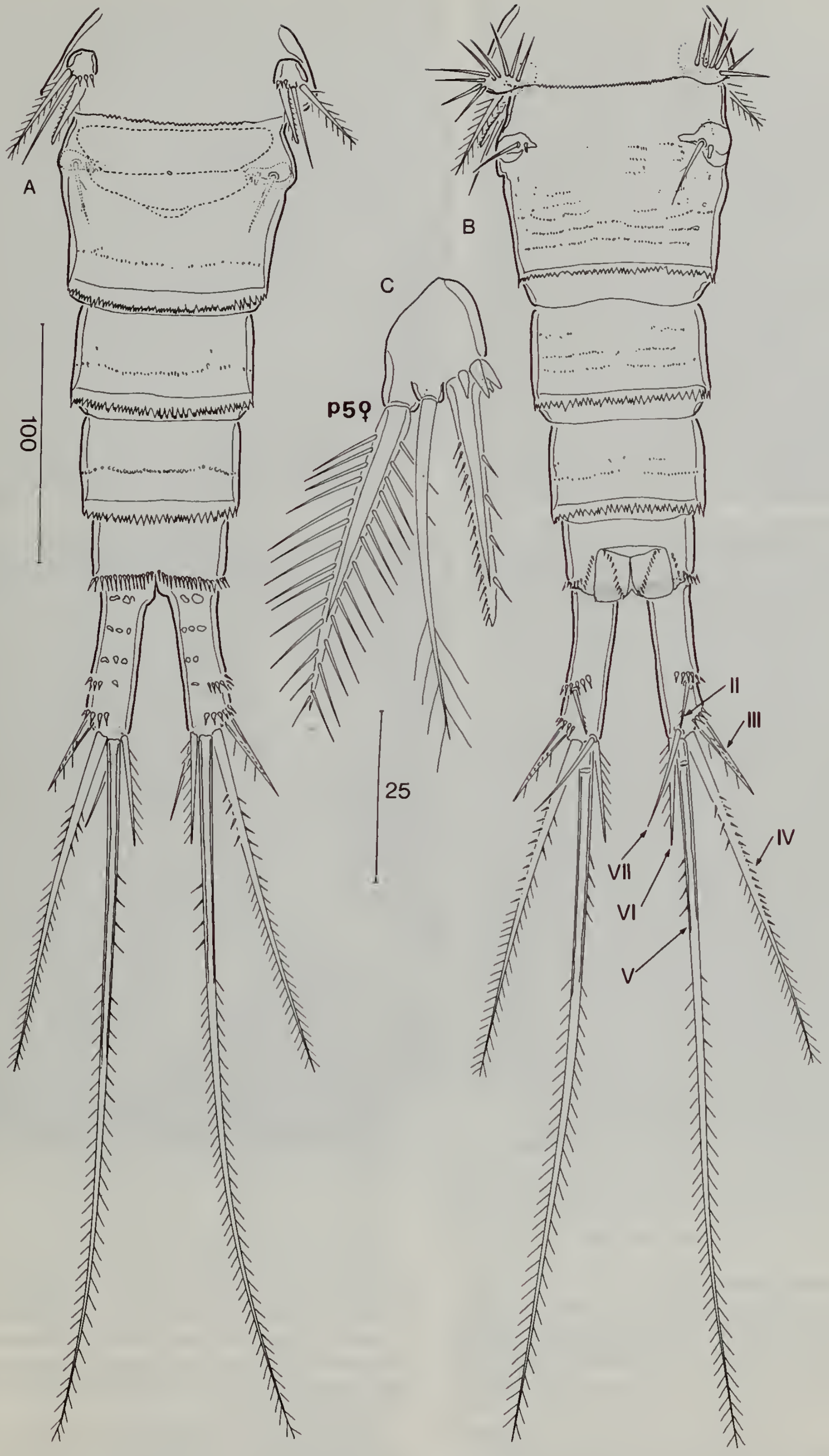

Fig. 18 *P. fimbriatus.* Adult female. A, urosome, ventral; B, urosome, dorsal. C, leg 5, ventral. Scale bars in μm.

	Coxa	Basis	Exopod	Endopod
Leg 1	0–1	1–I	I–1;I–1;III,1,4	0–1;0–1;1,I,4
Leg 2	0–I	1–0	I–1;I–1;III,I,5	0–1;0–2;1,I,4
Leg 3	0–1	1–0	I–1;I–1;III,I,5	0–1;0–2;1,I,4
Leg 4	0–1	1–0	I–1;I–1;III,1,4	0–1;0–2;1,II,2

Leg 6 represented by 1 plumose and 1 naked seta at posterolateral angle of second urosomite (Fig. 6E)

Male Copepodid V

Mean body length: mean ± standard deviation = 695 ± 44.83 µm (range 634 to 743 µm, n=7), mean body width 216 ± 8.1 µm (range 200 to 221.73 µm). Differing from male Copepodid IV as follows: body 9-segmented: first to fourth urosomites ornamented along posterior margins (Fig. 14B). Anal somite densely furnished with spinules along distal margin and extending either side of anal operculum.

Appendages as in fourth copepodid except as follows: antennule (Fig. 15B) 7-segmented; proximal 3 segments much enlarged, swollen (Figs 16C) first segment with one modified spiniform seta (stippled on Fig. 15B); segment 3 with 6 similarly modified elements and segment 4 with 1 such element. Setal formula; 19 + 1 spine, 5, 5 + 6 spines, 2 + 1 aesthetasc + 1 spine, 2, 3, 7 + 1 aesthetasc.

Leg 6 (Fig. 14B) represented by 3 setae, not visible in dorsal view.

Adult female

Body length: mean ± standard deviation = 935 ± 61.07 µm (range 833 to 1013 µm, n=10), mean body width 307 ± 14.9 µm (range 291 to 330 µm, n=10). Body (Fig. 17A) comprising 4-segmented prosome and 5-segmented urosome. Prosome with cephalothorax and 3 free pedigerous somites decreasing in width from anterior to posterior. Cephalothorax narrowing anteriorly; widest aproximately in middle. Third and fourth pedigerous somites with lateral groups of bristles at posterolateral angles. Urosome (Figs 18A,B) consisting of 5th pedigerous somite, genital double-somite and 3 free abdominal somites. Genital double-somite about as long as broad. Genital double-somite and first 2 free abdominal somites with surface ornamentation dorsally and ventrally : fifth pedigerous somite with ornamentation along posterior margin. Anal somite with spinular row ventrally extending round to anal operculum (Fig. 19A). Anal operculum smooth; row of spinules present in anal cleft either side of midline (Fig. 19D).

Caudal rami about 3.5 times longer than broad with ornamentation comprising rows of pits or cuticular depressions on ventral surface (Fig. 19B). Generally held wide apart, slightly divergent. Caudal rami with 6 setae; seta I missing; outer lateral seta (III) with spinular row at base extending dorsally and ventrally; small seta (II) on dorsolateral surface with spinular row behind it and extending ventrally.

Antennule 8-segmented (Fig. 17B), quite short. First segment with spinular row ventrally. Segment 2 with partial suture line. Fourth segment longest. Segment 5 distinctive with short aesthetasc (Fig. 16B); apical segment with aesthetasc fused to adjacent seta at base (Fig. 16E). Setal formula: 8, 12, 6, 5, 2 + 1 aesthetasc, 2, 3, 7 + 1 aesthetasc. One element on seventh segment possibly a setiform aesthetasc (see discussion below).

Antenna 4-segmented (Fig. 8F), comprising coxobasis and 3-segmented endopod. Coxobasis with complex ornamentation as figured and armed with 2 inner setae, and 1 outer spinulose seta representing exopod. First endopodal segment with inner distal seta and midsurface spinular row. Second endopodal segment with 9 setae, of which 5 on inner margin and 4 arranged along inner part of distal margin; segment ornamented with spinules along outer margin. Third endopodal segment armed with 7 setae around apex; segment ornamented with spinular row along outer margin.

Labrum with complex ornamentation on ventral surface (Fig. 20A). Anterior part broader than posterior part. Posterior margin forming strong teeth.

Mandible (Fig. 20B) consisting of well developed coxal gnathobase and reduced palp. Gnathobasic blades mostly simple, dorsal seta with spinules along inner rim. Palp represented by 3 setae, one long and spinulose, the other plumose. Third seta short and naked. Central surface of coxa with 3 spinular rows and another spinular row on margin at base of gnathobase.

Maxillule (Fig. 20C) consisting of powerful praecoxa and reduced 2-segmented palp. Praecoxal arthrite armed with 7 setae articulating at base and 4 spines fused to segment; proximalmost seta spinulose, spines naked. Proximal segment of palp derived from coxa and basis, bearing 2 naked and 1 spinulose inner margin setae, plus outer seta representing exopod. Distal segment of palp, representing endopod, armed with 2 setae with spinules along margin and 1 naked seta.

Maxilla 5-segmented (Fig. 20D), comprising praecoxa, coxa, basis and 2-segmented endopod. Praecoxa with spinular row on outer margin. Praecoxal endite with 2 setae, 1 of which spinulose. Coxa with proximal endite represented by single seta, distal endite with well developed process carrying strong spinulose seta and naked seta apically. Basis drawn out into powerful spinulate claw and armed with strong accessory claw with spinular row along convex margin and naked seta. First endopodal segment carrying 2 spinulose setae, second carrying 3 setae.

Maxilliped 4-segmented (Fig. 20E), comprising syncoxa, basis and 2-segmented endopod. Syncoxa armed with 3 inner margin setae representing endites; ornamented with spinular row near middle of inner margin and 2 spinules on outer margin. Basis armed with 2 inner setae, 1 of which with spinules; ornamented with 2 transverse rows of spinules near outer distal angle and another spinular row midway along outer margin. First endopodal segment bearing claw-like seta with 5 spinules at midlength. Second endopodal segment with 3 setae, 2 of which bearing spinules midway; outermost naked.

Legs 1 to 4 each with complex ornamentation on anterior and posterior surfaces of coxa as figured; also ornamented on intercoxal sclerite. Legs 1 to 3 with spinular rows on posterior surface of exopodal segments 1 and 2, and endopodal segment 2.

Leg 1 (Fig. 10F) with 3-segmented protopod. Praecoxa represented by triangular sclerite at outer proximal angle. Coxa with inner plumose seta. Basis with outer angle seta and setiform spine on inner margin; bearing spinular row on posterior surface. Both seta and spine with spinular rows at bases.

Legs 2 (Fig. 11F) and 3 (Fig. 12E) with 3-segmented protopods. Coxa with inner setiform spine. Outer seta on basis with spinular row at base. First segment of exopod with spinular row on anterior surface.

Leg 4 (Fig. 13D) with 3-segmented protopod. Praecoxa represented by thin, hooped sclerite. Coxa with inner setiform spine. Basis with outer seta bearing spinular row at base; spinular row on inner margin anteriorly. Segments 1 and 2 of

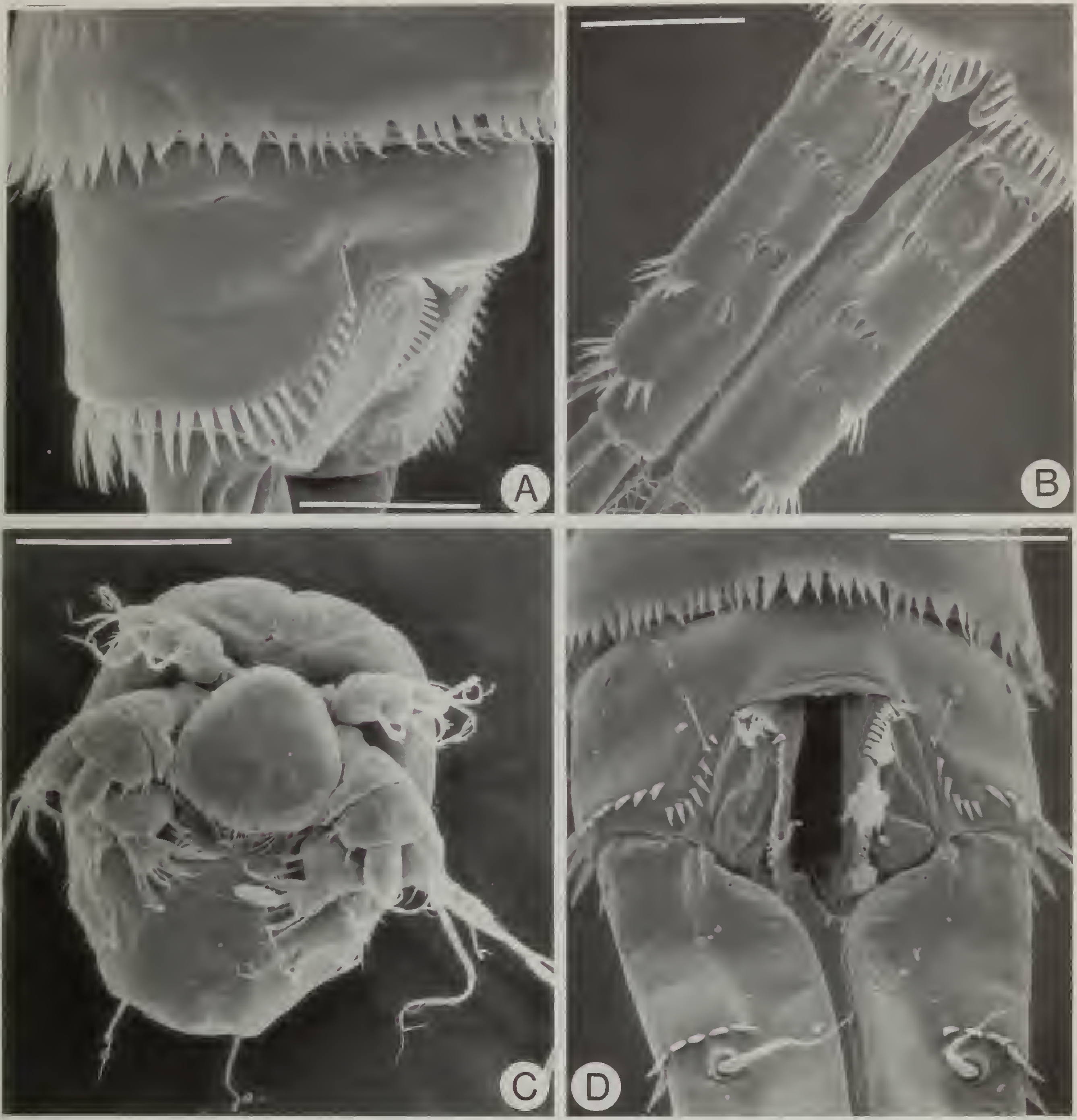

Fig. 19 Scanning electron micrographs of *P. fimbriatus.* A, Adult female, anal operculum, lateral; B, adult female, caudal rami showing ornamentation of pits in integument; C, Nauplius II, ventral; D, Adult female, anal operculum, dorsal. Scale bars A = 20 µm, B = 40 µm, C = 60 µm, D = 25 µm.

exopod with spinular row on distal margin anteriorly. Spine and seta formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0–1	1–I	I–1;1–1;III,1,4	0–1;0–1;1,1,4
Leg 2	0–I	1–0	I–1;I–1;III,I,5	0–1;0–2;I,I,4
Leg 3	0–1	1–0	I–1;I–1;III,1,5	0–1;0–2;I,I,4
Leg 4	0–1	1–0	I–1;I–1;II,I,5	0–1;0–2;1,II,2

Leg 5 (Fig. 18C) comprising single free segment, armed with 1 well developed outer spinulose seta, 1 strong inner spine ornamented with spinules, and 1 plumose seta in middle. Leg 6 (Fig. 18A) represented by 1 naked seta and 1 tiny spinule dorsolaterally.

Adult male

Body length: Mean ± standard deviation = 732 ± 47.45 µm (range 673 to 769 µm, n=10), mean body width 237 ± 7.6 µm

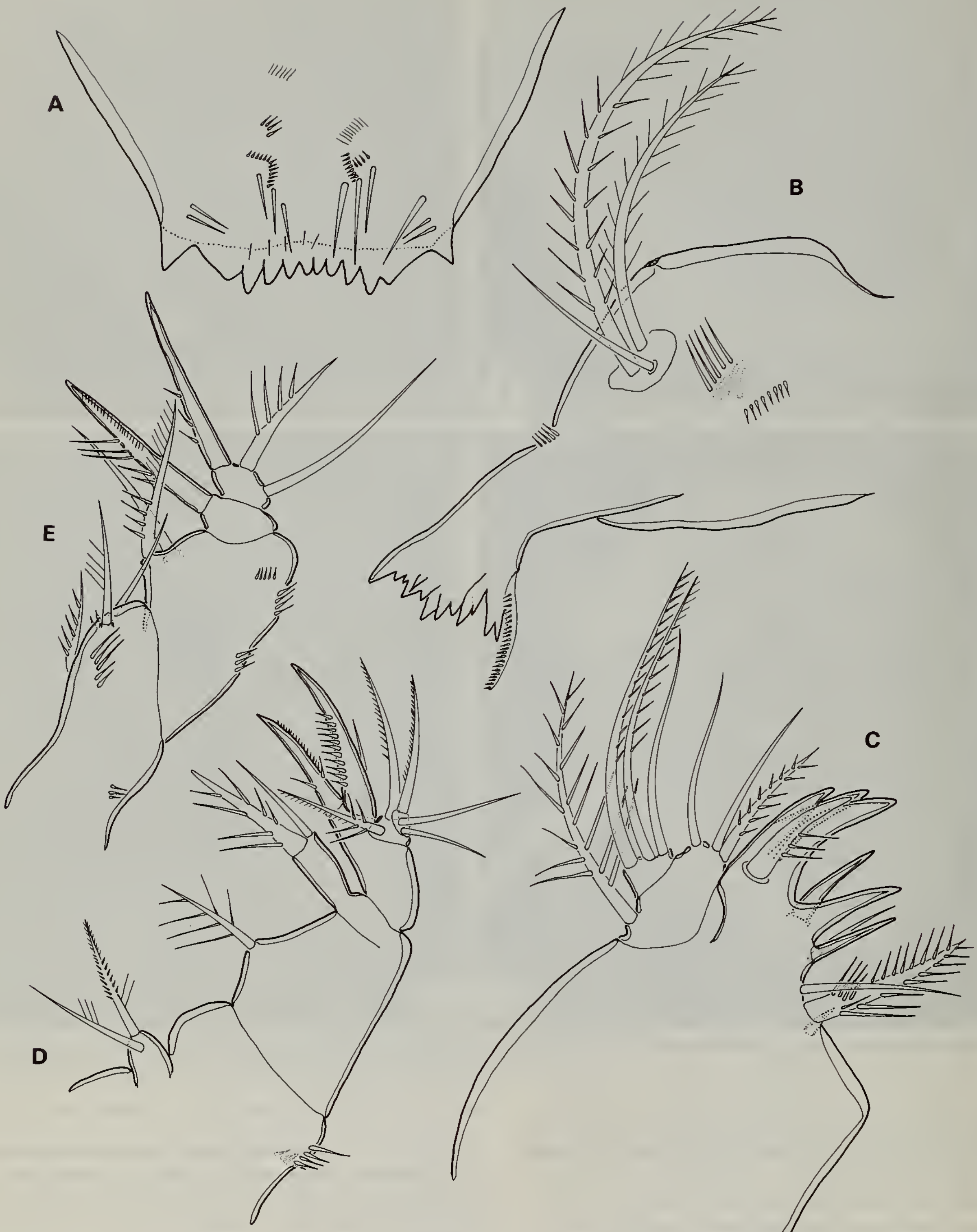

Fig. 20 *P. fimbriatus.* Adult female. A, Labrum, ventral; B, Mandible, posteroventral; C, Maxillule, ventral; D, Maxilla, posterior; E, Maxilliped, anterior. Scale bar in µm.

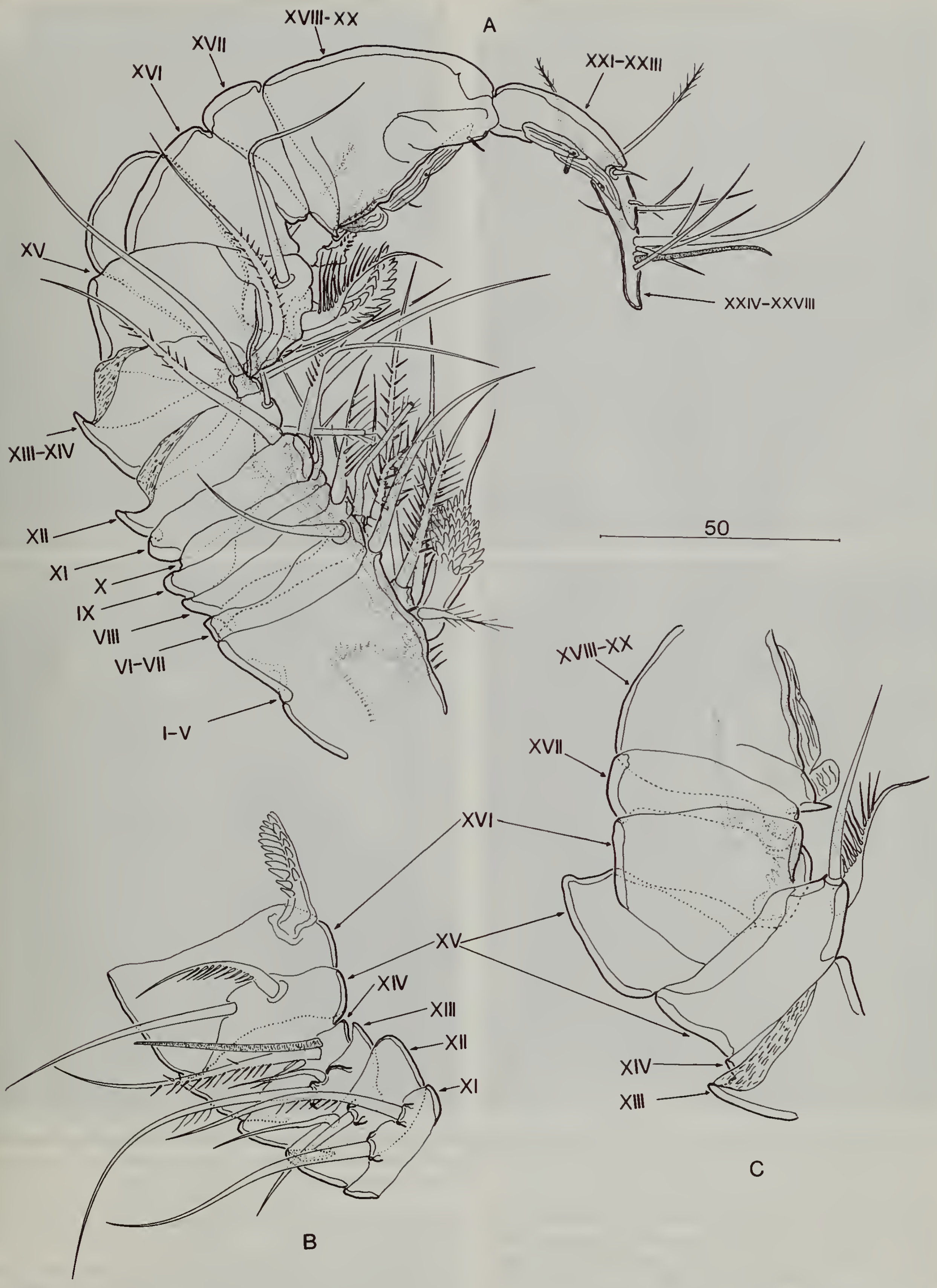

Fig. 21 *P. fimbriatus.* Male antennule. A, dorsal view. B, Detail of segments XI to XVI, anterior; C, Detail of segments XIII to XX, lateral view. Scale bar in µm.

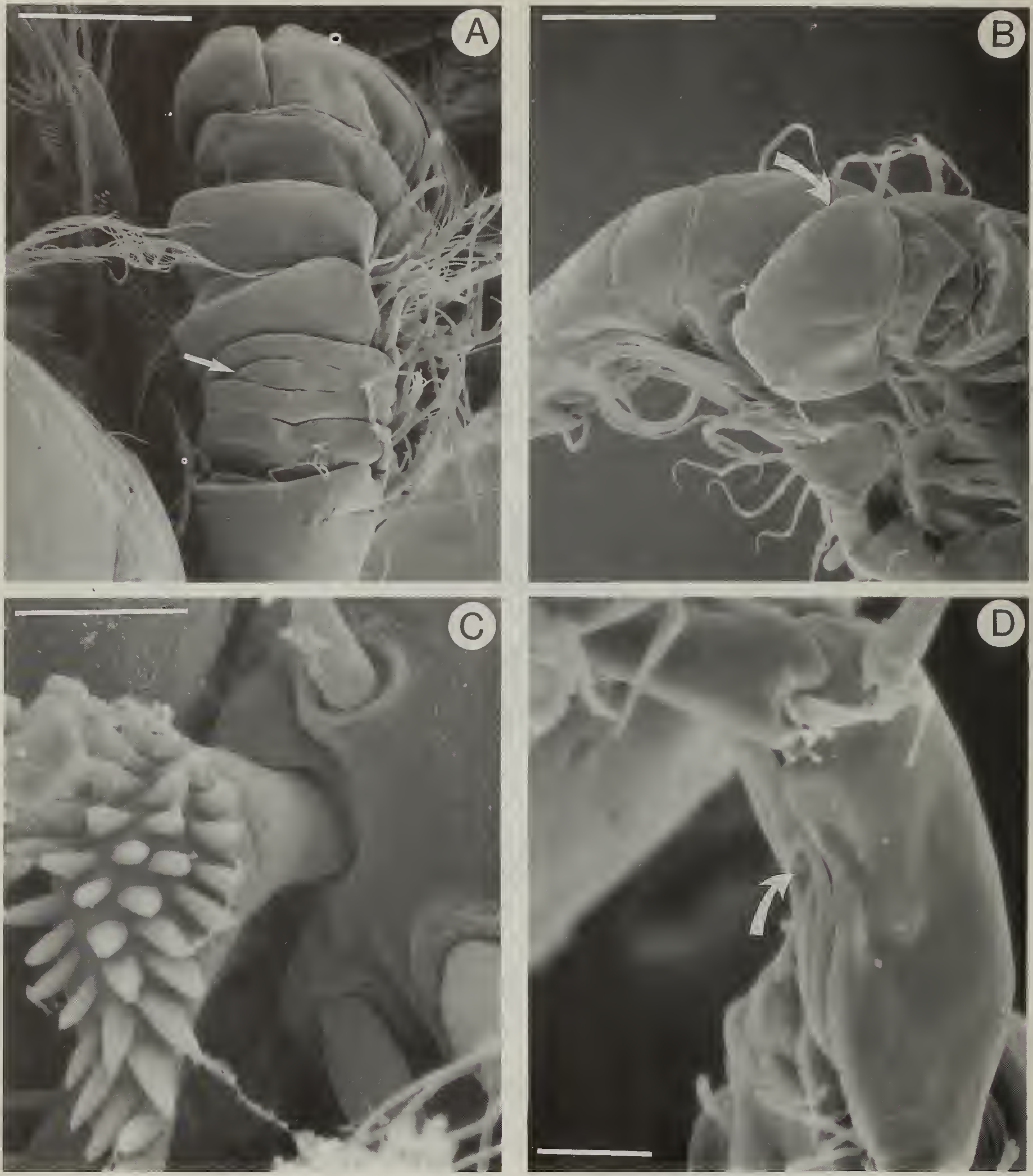

Fig. 22 Scanning electron micrographs of *P. fimbriatus*. Adult male antennule. A, Dorsal view, with segment 5 arrowed; B, Lateral view, with sheath on segment XV arrowed; C, Modified seta on proximal segment; D, Segment proximal to geniculation, with pore on modified element arrowed. Scale bars A = 30 µm, B = 25 µm, C = 6 µm, D = 5 µm.

(range 226 to 247 µm, n=10). Body (Fig. 17C) differing from adult female as follows: urosome 6-segmented, comprising fifth pedigerous, genital and 4 free abdominal somites; ornamentation of spinule rows as in Fig. 14D. Genital somite bearing paired genital apertures ventrally (Fig. 14C).

Caudal rami about 2.5 times longer than broad, ventral surface unornamented. Large medial seta (V) relatively longer than in female.

Antennule 15-segmented (Figs 21A-C). Segment 1 armed with 9 setae; 1 seta large and modified (Fig. 22C), by ornamentation of strong spinules in proximal and mid sections, tapering to fine point distally; segment ornamented with curved row of long spinules and row of minute spinules. Segment 2 with 4 setae. Segment 3 with 2 setae. Segments 4 and 5 partly fused, with segment 5 (arrowed in Fig. 22A) defined only on dorsal side, not ventrally. Segment 4 with 2 setae; segment 5 with 2 setae. Segment 6 with 2 setae. Segments 7, 8 and 9 separated from each other by extensive arthrodial membrane: segment 7 with 2 setae, segment 8 with 2 setae, and segment 9 with 2 setae plus aesthetasc. Segment 10 (= ancestral segment XV) produced on one side into extensive sheath (arrowed in Fig. 22B) enclosing segment 11 ventrally; armed with 2 setae, 1 ornamented with long spinules unilaterally. Segment 11 bearing curved seta ornamented with double row of strong denticles, plus 1 naked seta. Segment 12 partly fused to segment 13; armed with short seta ornamented with 2 rows of fine spinules, plus short naked seta. Segment 13 partly subdivided by partial suture: armed with short spinulate seta proximally, 2 short naked setae, plus 1 modified element attached to segment by short stalk, main part of element lying along surface of segment and ornamented with longitudinal ridges and small central pore (arrowed in Fig. 22D). Geniculation located between segments 13 and 14. Segments 14 and 15 partly fused, forming curved subchela-like section: segment 14 armed with 1 seta, 1 aesthetasc and 2 modified elements each ornamented with longitudinal ridges and a central pore, as distal element on segment 13. Apical segment tapering distally; armed with 11 setae and 1 aesthetasc, mostly originating on outer (= posterior) surface.

All other appendages as in female except for fifth (Fig. 14E) and sixth legs (Fig. 14F). Outer spinulose seta of leg 5 ornamented with some long setules distally. Sixth legs forming opercular plates bearing row of large spinules along ventral surface; armed with 1 inner spine, 1 well developed spinulose seta and 1 inner naked seta.

DISCUSSION

The number of naupliar instars in the Cyclopoida has been the subject of some controversy but it is clear, as Elgmork & Langeland (1970) strongly indicated, that there are normally 6 naupliar instars. This is supported by recent works on free-living freshwater Cyclopoida by Dahms & Fernando (1992, 1993, 1994) and by our data. The most difficult distinction is between nauplius IV and V and these stages have often been confused.

The complete naupliar sequence of *P. fimbriatus* was previously described by Ewers (1930) and Dukina (1956). Nauplius I and II were also described by Gurney (1933) but none of these provides setation counts of sufficient accuracy. Ewers (1930) described 6 stages but our descriptions differ as follows: antennule is 3-segmented not 4-segmented; antennary exopod is 4-segmented at N I and becomes 6-segmented, rather than remaining 4-segmented; caudal rami of N IV are represented by 2 pairs of setae and 1 pair of minute seta, rather than just 2 pairs of setae; ventral body surface is ornamented with spinular rows throughout the nauplius phase. In general, however, Ewers' drawings are so small that it is not worthwhile making detailed comparisons of appendage setation patterns.

Six naupliar stages were also described by Dukina (1956). Our descriptions differ from Dukina's as follows: antennule is 3-segmented; antennary exopod is 4-segmented at N I (given as 5-segmented by Dukina). Dukina's descriptions of appendage setation also lack sufficient detail for meaningful comparisons.

Gurney (1933) described the first 2 naupliar stages, but our findings indicate that the caudal rami of N II are represented by a pair of setae not by 2 pairs as illustrated by Gurney. Apart from this discrepancy our results differ only in that the exopod of antenna is described as 3-segmented rather than 4-segmented as in our material.

The copepodid stages of *P. fimbriatus* were also partly described by Gurney (1933). Although our results are in substantial agreement, for example, with antennulary segmentation throughout the copepodid phase, Gurney's drawings are not sufficiently accurate to permit comparisons of segmental setation.

Analysis of the antennulary setation patterns of adult male *Paracyclops* permits the identification of the pattern of segmental homologies. The basic armature of each antennulary segment in copepods is 2 setae plus one aesthetasc (Giesbrecht, 1892), with a few exceptions as identified by Huys & Boxshall (1991). Using this basic pattern, the 9 setae on the first segment of male *P. fimbriatus* indicate that it can be identified as representing 5 ancestral segments (segments I–V). The second segment, with 4 setae, can similarly be identified as derived from 2 ancestral segments (VI–VII). The third to twelfth segments all represent single ancestral segments (VIII to XVII), as indicated by the presence of a maximum of 2 setae on each. The fourth and fifth are incompletely separated (Fig. 22A) but we have treated them as distinct. The thirteenth segment has only 4 setae but is here identified as representing 3 ancestral segments (XVIII–XX). This decision is based on the presence of the neocopepodan geniculation between the thirteenth and fourteenth segments which unequivocally identifies the segmental boundary involved as XX to XXI, and on comparison with other cyclopids such as *Euryte robusta* Giesbrecht, 1900. In *E. robusta* males segment XVIII is separate and carries a long naked seta and a short spinulose seta, segment XIX–XX carries a short spinulose seta and a modified spine proximally and a slender seta distally (Huys & Boxshall, 1991). In *P. fimbriatus* the proximal part of the triple segment is defined by a partial suture marking the original plane between segments XVIII and XIX–XX. This part carries only a single spinulose seta and lacks the long seta; the distal part representing XIX–XX carries the same setation as in *E. robusta*. This confirms our interpretation of the thirteenth segment as a triple segment (XVIII–XX). The fourteenth and fifteenth segments, lying distal to the geniculation represent ancestral segments XXI–XXIII and XXIV–XXVIII, exactly as Huys & Boxshall (1991) found for *E. robusta*.

Compound antennulary segments, such as the first and second segments of *P. fimbriatus*, were simply referred to as 'fused' by Huys and Boxshall (1991) in their comparative analysis of antennulary segmentation patterns in all copepod orders, although such compound segments could be the result of two different developmental processes:

1) secondary fusion of segments that were separated earlier during ontogeny

2) failure of separation during development.

The compound first and second segments of the male antennule of *P. fimbriatus* result from the second process, the failure to separate. In contrast, the compound apical segment results from the secondary fusion of the sixth, seventh and eighth segments of the copepodid V stage. (The eighth segment of the copepodid V was already a compound segment, representing three ancestral segments XXVI–XXVIII which are not separately expressed by any known member of the order Cyclopoida).

Vertical tracking of the segmental boundaries as identified by their setation elements allows us to identify the homologies of

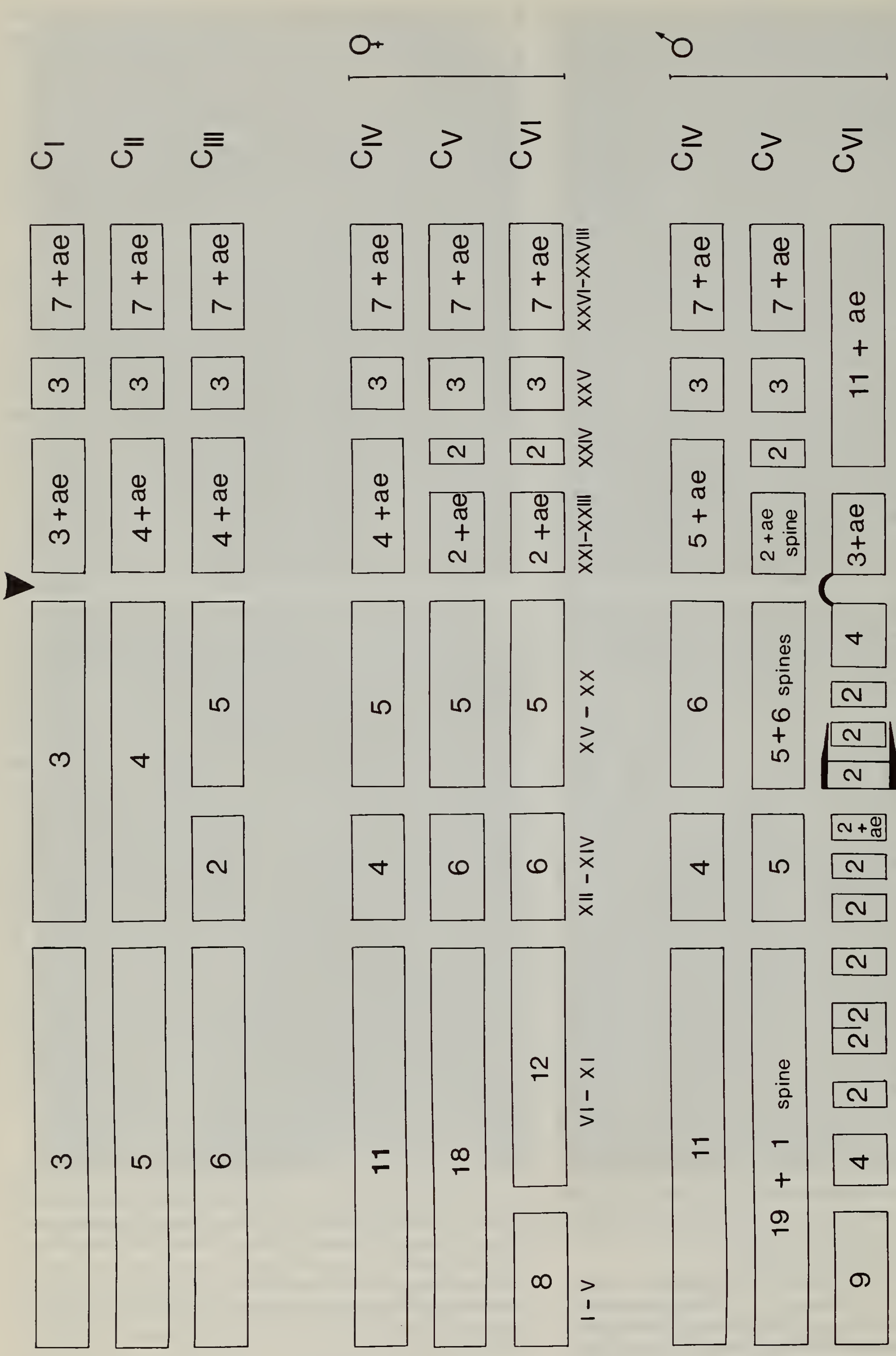

Fig. 23 *P. fimbriatus.* Schematic comparison of antennulary segmental homologies in all copepodid stages of both sexes; showing location of geniculation and sheath in adult male as well as numbers of setae, spines and aesthetascs (ae) in all stages. [Roman numerals indicate derivations from hypothetical 28-segmented ancestral antennule proposed by Huys & Boxshall (1991); C_{VI} = adult.]

the segments of the female antennule and of the antennules throughout the copepodid phase of development. These results are presented in schematic form in Figure 23 which visually indicates homologous segmental boundaries expressed in successive copepodid stages. The aesthetasc derived from ancestral segment XXI provides a reference point throughout the copepodid phase: from the third segment of the first copepodid, to the fifth segment of the adult female and the fourteenth segment of the adult male. This, in concert with other setation features, confirms the unequivocal identification of the XX to XXI articulation (marked by the large arrow) in all stages. Identification of the homology of the more proximal segments relies on the presence of 11 setation elements on the third segment of the male copepodid V stage. These 11 elements testify to the segment's derivation from 6 unseparated ancestral segments (XV–XX) and indicates that the boundary between the second and third segments represents the XIV to XV articulation. Similarly, the presence of 5 setae on the second segment indicates that the boundary between first and second segments represents the XI to XII articulation. The remaining segmental homologies in all stages, including the adult female, can now be identified by tracking vertically through the male stages back to copepodids I and II and then forwards again to the adult female.

The seventh segment of the female antennule is identified as homologous with a single ancestral segment (XXV). The presence of 3 setae on this segment therefore requires explanation since the basic armature of segment XXV is 1 posterior margin seta plus 1 seta and 1 aesthetasc on the anterior margin (Huys & Boxshall, 1991). We suggest that one of the anterior elements may be a setiform aesthetasc and this should be investigated ultrastructurally.

This is the first time that the homologies of all antennulary segments have been identified in all copepodid stages of both sexes of any cyclopoid copepod, with reference to the hypothetical 28-segmented antennule of the ancestral copepod (Huys & Boxshall, 1991). Within the family Cyclopidae antennulary segmental numbers are frequently reduced and, indeed, many genera are characterised by their low segment numbers. The possible involvement of heterochrony in the reduction of antennulary segmental numbers has already been noted. Gurney (1933) suggested that 'the reduced numbers of antennulary segments in some species may be accounted for as the persistence of a larval character in the adult', pointing out that during development the last copepodid (Co V) typically has an 11-segmented antennule and that this number is commonly found in adults, as for example in *Microcyclops*.

Several authors working on cyclopids were aware of the importance of determining homologies between the different generic segmentation patterns and made detailed comparisons. Gurney (1933) reviewed earlier work by Claus (1893), Manfredi (1923), Lucks (1929) and Gelmini (1928) on the sequence of segmental subdivision during development in *Cyclops* species. He presented a tabular system showing derivations of a 17-segmented antennule and confirmed this pattern using his own data on *C. strenuus*. The strict determination of ancestral homologies of antennulary segments provides new insight into the rather confused world of cyclopid systematics at the generic level.

The scheme of segmental development (Fig. 23) indicates that at the moult from copepodid II to copepodid III it is the second segment that subdivides. This contrasts with the scheme presented for *P. fimbriatus* by Gurney (1933) who showed the first segment subdividing at this moult. We base our interpretation on the positions and relative lengths of the setae on these segments. In particular a relatively long seta is positioned at the anterodistal angle of the first segment in copepodid II and 2 similarly long setae are present at the same position in copepodid III. Since no other setae of this length are present we interpret this as evidence of the constancy of the boundary marked by this seta and therefore conclude that the second segment has subdivided.

The setation of the second endopodal segment of the antenna increases progressively through the copepodid stages of *P. fimbriatus* in a very regular manner. The first copepodid stage possesses 4 setae distributed around the inner-distal angle of the segment (Fig. 8A). The seta which is located on the angle is slightly stouter than the other 3 and is here identified as seta VIII, using the numbering scheme proposed for another member of the family Cyclopidae by Boxshall & Evstigneeva (1994). The more distal seta is then identified as seta IX and the 2 more proximally located setae on the inner margin, as setae VII and VI. These 4 setae are presumably homologous with the proximal group of 4 setae present on the margin of the unsegmented endopod of the sixth nauplius stage (Fig. 3F). At each successive moult through the copepodid phase one additional seta is added proximally on the inner margin of the segment (Figs 8A-F). Thus at copepodid II a fifth seta (seta V) is added, at copepodid III a sixth seta (seta IV), and so on, until the final moult to adult (= copepodid VI) at which the ninth and final seta (seta I) is added.

The progressive development of the setation suggests that reductions in numbers of setae on the second endopodal segment, which are common within the family Cyclopidae, may be interpreted as resulting from heterochronic events. *Cryptocyclops bicolor* (Sars, 1863), for example, is a cyclopid with only 7 setae on the second endopodal segment. This number is typical of the copepodid IV stage in both *Paracyclops* and the presumed ancestral cyclopid stock, and may be interpreted as evidence that a neotenic event within the *Cryptocyclops* lineage has interrupted the progressive addition of setae.

The ontogeny of copepodid stages and examination the patterns of leg formation offer some evidence for inferring copepod phylogenetic relationships (Ferrari, 1988). A common pattern of development for legs 1–4, exhibited by at least 20 genera, was recognized by Ferrari. The pattern of development for the swimming legs of *P. fimbriatus* is in accordance with this common pattern as follows:

Legs	1	2	3	4
N	1ˆB;	1ˆB		
I	1+1;	1+1;	1ˆB	
II	2+2;	2+2;	1+1;	1ˆB
III	2+2;	2+2;	2+2;	1+1;
IV	2+2;	2+2;	2+2;	2+2;
V	3+3;	3+3;	3+3;	3+3;
VI	3+3;	3+3;	3+3;	3+3;

(Where N = nauplius; Roman numerals = copepodid stages; 1ˆB = primary leg bud; 1+1 = reorganized leg with 1-segmented exopod and endopod; 2+2 = leg with 2-segmented exopod and endopod; 3+3 = leg with 3-segmented exopod and endopod).

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